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Observations of the reproduction and population structure of the caenogastropod, *Gabbia vertiginosa* Frauenfeld, 1862 (Rissooidea : Bithyniidae)

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Abstract

Aspects of the reproduction and population structure of *Gabbia vertiginosa* (Bithyniidae) in the New England Tablelands, New South Wales, Australia, are described. The pattern of embryo growth from encapsulation in the pallial oviduct, deposition of fully formed embryonic snails in the habitat, to sexual maturity in the adult snail are examined. A three-year population study has shown the reproductive period of *G. vertiginosa* to commence in December and end in June/July with the possibility of three reproductive events per season.

Additional keywords: Bithynia, embryo.

Introduction

Gabbia vertiginosa Frauenfeld, 1862 (= *Gabbia australis* Tryon, 1865) is one of Australia's representatives of the family Bithyniidae (Caenogastropoda : Rissooidea) (see Ponder 2003). Other members of the family for which biological information is available are *Bithynia leachi* (Sheppard, 1823), *Bithynia tentaculata* (Linnaeus, 1758) and *Bithynia graeca* (Westerlund, 1879) (Lilly 1953; Graham 1971; Eleutheriadis and Lazaridou-Dimitriadou 1995). Most members of the family possess a calcareous operculum and prefer slow moving rivers, ponds and swampy backwaters where they live on and within vegetation in shallow, muddy substrates (Fretter and Graham 1962; McMichael 1967; Graham 1971; Ponder and De Keyzer 1998).

The shell colour of *G. vertiginosa* is a light horn, sometimes with a greenish tinge that is particularly evident on specimens collected from stagnant ponds (pers. obs.). Dark pigment contained within the epithelium of the animal is visible through the shell except in those snails that have passed through a rest period in adulthood (pers. obs.). The Bithyniidae filter feed and browse on the contents of ruptured plant cells, detritus and decaying weed (Lilly 1953). A freshwater plant common in aquatic habitats in eastern Australia, *Elatine gratioloides* (Elatinaceae), is used by *G. vertiginosa* in the New England Tablelands for food, shelter and deposition of egg capsules (pers. obs.). The distributional range of *G. vertiginosa* extends from the eastern areas of New South Wales from Sydney to southern Queensland (Ponder 2003).

Until Ponder's (2003) monograph of the Australian species, only a small amount of data on *G. vertiginosa* had been available. Simpson and Stanisic (1986) briefly discussed its ecology and distribution in the New England area and some information was provided by Ponder and De Keyzer (1998) in their overview of the family (see also Smith and Kershaw 1979). A series of observations and studies of *G. vertiginosa* were undertaken in this study to describe the reproduction and the population structure of the species. Larvae of

trematode parasites found within snails examined during the study are described in Koch (2002, 2003, in press *a*, in press *b*).

Materials and methods

Snail collections

One particular site was chosen within the New England Tablelands for a medium-term study of *G. vertiginosa*. Within this habitat (Saumarez Road swamp, 5 km south south-west of Armidale, New South Wales, Australia: 31°50′S; 151°30′E) a large population of *G. vertiginosa* had been observed during 1999. Surveys of the snail population at this site were conducted in January, March, July and November of each year commencing July 2000 and ending in January 2003. The study area was 8 m in length and 0.5–1.5 m in width. This area was divided into 160 5-cm wide transects running from the shoreline out, with transect 0 at the northern end and transect 160 at the southern end of the habitat. Transects were chosen at random at each survey period using a table of random digits (Rohlf and Sokal 1969). The number of transects required for each survey was determined in a pilot study (March 2000) using the ratio estimation method for selecting sample units that are of irregular shape or length (Caughley and Sinclair 1994). Twelve transects were taken at each survey. Specially constructed wooden rectangles were used to mark out each transect during collection. All snails present in each transect were collected by careful and systematic sifting through the substrate and weed by hand with the intention of disturbing the habitat as little as possible. They were then placed in marked jars containing pond water for transportation to the laboratory. Sampling without replacement was the method of collection used for each survey (Sutherland 1996). During the study period, 4736 *G. vertiginosa* snails were collected. Voucher specimens are lodged in the Australian Museum (C.433803–C.433807).

Snails were dissected by carefully breaking away the shell and the tissue was examined in a cavity block under a stereomicroscope. Whole specimens were either placed immediately into absolute ethanol for future molecular studies, or in 10% neutral buffered formalin. All parasite larvae found during snail observations and dissections (another aspect of this study) were either preserved or used for infection experiments to obtain the adult worms for correct taxonomic placement of the species (see Koch 2002, 2003, in press *b*).

Water quality testing of pond water at surveys of the site was done using an Aquamerck 8024 kit produced by Merck KgaA Co. (Munich, Germany). Measurements are given in mm unless otherwise stated and, where ranges are shown, the mean is noted in parentheses.

Laboratory breeding

Larval capsules of *G. vertiginosa* (150 embryos in total) were found attached to snails and vegetation collected from Saumarez Road swamp. These capsules were retained in small glass bowls containing filtered pond water until hatching occurred and snail shell size had reached ≈ 3 mm. At this point, all snails were transferred to aerated aquaria where growth in their shell length was measured daily and recorded.

Aquaria were maintained in a laboratory open to natural light and ambient temperatures in order to closely simulate normal environmental conditions and photoperiods. Water temperatures in the aquaria ranged from 22°C between November 2000 and March 2001, to 5°C during the autumn/winter months April to June 2001 (≈ 4°C higher than average water temperatures during winter periods on the New England Tablelands (Bureau of Meteorology Australia 2002)). Snails were fed *Elatine gratioloides* collected from the habitat and commercial fish flakes and pellets. Flakes and pellets were only used when *E. gratioloides* was unavailable. At Day 220, the laboratory-bred snails were dissected and shell size and development of the reproductive organs were noted and compared against the data collected from *G. vertiginosa* harvested during surveys at the study site at Saumarez Road swamp.

Size and age measurements

Shell length (apex to the anterior tip of the aperture) was used as a guide to age and sexual maturity for both laboratory-bred snails and those taken from the natural habitat. Measurements were taken using Vernier calipers (Krist 2000). For the purposes of this study, embryos were defined as the developing snails contained within capsules, from the time of deposition on substrates to hatching from capsules (≈ 0.05–0.3 mm shell length). Juveniles were defined as those snails ranging from hatchlings (≈ 0.3 mm) to ≈ 4.5 mm shell length; snails greater than 4.5 mm shell length were classified as adults. Sexual maturity was defined as the presence of a fully formed seminal receptacle and an ovary in females and, in males, a mature seminal vesicle and testis, as studied under a light microscope.
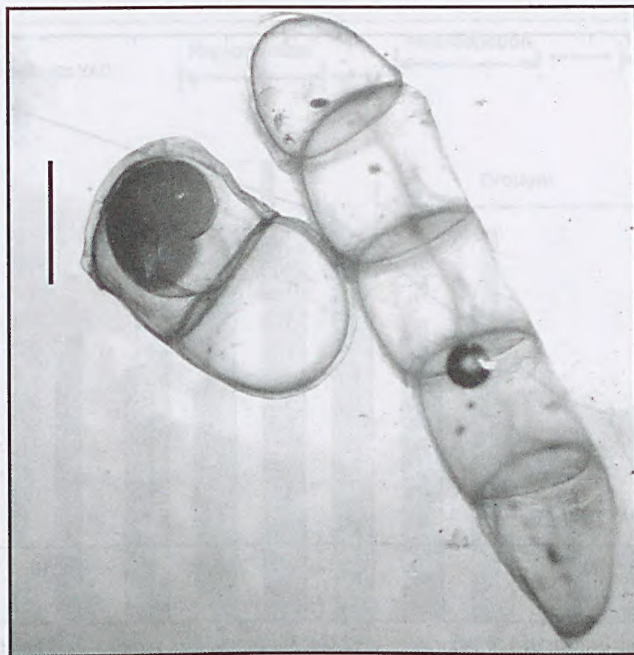
Fig. 1. Preserved capsules of *Gabbia vertiginosa* collected from Saumarez Road swamp, Armidale, New South Wales. One capsule still contains an embryo at ~30 days after deposition; the others have hatched. Scale bar = 0.05 mm.

Results

Pre-deposition

As the embryos mature within the female, they travel along the ventral channel of the pallial oviduct towards the genital aperture. At this point in their development, the embryos had a basic snail-like appearance with the exception of the growth of the shell, which was just commencing. Once the genital aperture was reached, the embryos were encased in fully formed capsules in strings, ready for deposition on the substrate or the shell of other snails. The shell on embyros was translucent and the operculum present.

Deposition to hatching

Embryo casings consisted of two to six compartments in single strings, one embryo per compartment (Fig. 1). Embryos were translucent for about 25 days after deposition and then became opaque, although the shell remained translucent during encapsulation. Mean shell size at deposition was 0.05 mm. The deposition to hatching period was 30–34 (32) days at 22°C, during which embryonic movement could be observed when the capsules were touched.

Post hatching

Figure 2 shows the mean growth of the snails over 220 days from time of hatching. Shell size increased from 0.25–0.3 (0.275) mm to 0.3–0.4 (0.35) mm by Day 4. At Day 5,
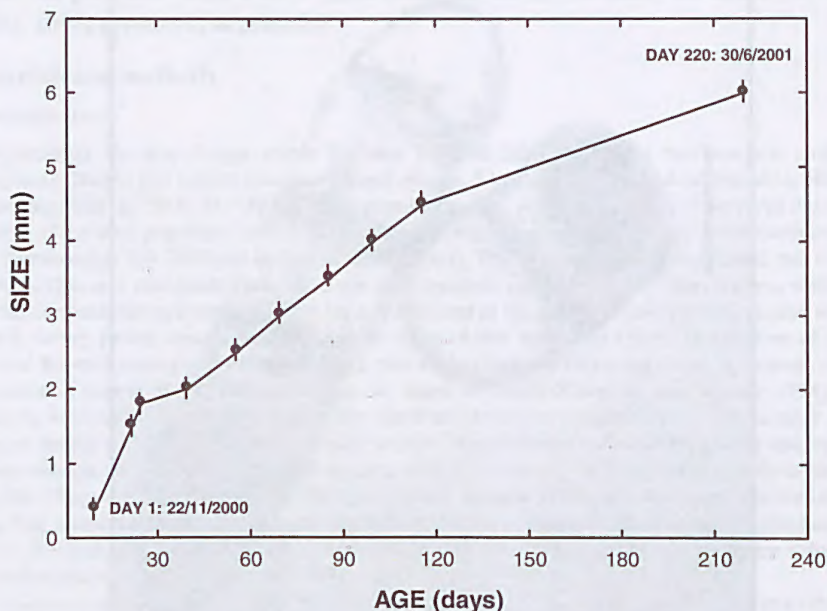
Fig. 2. Mean growth of 150 laboratory-bred *Gabbia vertiginosa* (size as shell length) over 220 days at 22°C (22 November 2000 to 30 June 2001) from newly hatched snails to sexual maturity. Error bars indicate standard deviations in snail shell lengths at each recorded day.

colouration of the shell had commenced from the apex of the whorl and down towards the outer lip of the aperture. Black pigment was also formed in the mantle and epithelial tissues. Sexual dimorphism became obvious at Day 19 (mean shell size 1.2 mm). The penis had differentiated and testicular tissue had acquired a pale orange colouration although neither the seminal vesicle nor seminal receptacle was developed. The mantle tissue was black and the rectum and faecal pellets within it were visible. By about Day 21, darkening of the shell had extended over the entire height of the spire (mean shell size 1.8 mm). Colouration of the shell was complete by about Day 35 (mean shell size 2.0 mm). Sexual maturity was complete in both sexes at about Day 135 (mean shell size 4.5 mm) with the largest shells reaching a mean of 6.0 mm by 220 days. Maximum life span of laboratory-bred snails was 20 months (mean 18 months).

Population structure over time

Analyses of quarterly snail collections and dissections between July 2000 and January 2003 showed the reproductive period of *G. vertiginosa* commenced in late December to early January and ended in late June to early July of each year. The appearance of embryos in January 2001 and the corresponding peak in the 0.3–2.0 mm size category in March 2001 paralleled the timeline (45–50 days) of laboratory-bred snails during the same growth phase from embryos to juveniles of mean shell length 2 mm (Figs 2, 3). A peak in the adult size class would be expected in July 2001 if development of field juveniles to sexual maturity (mean shell size 4.5 mm) continued to parallel laboratory growth timelines. The absence of this expected peak in the field suggests the species had high recruitment but low survival of juveniles leading into the winter of 2001. Declines in population densities are presumably part of the natural cycle of reproduction in a habitat with a diversity of climatic
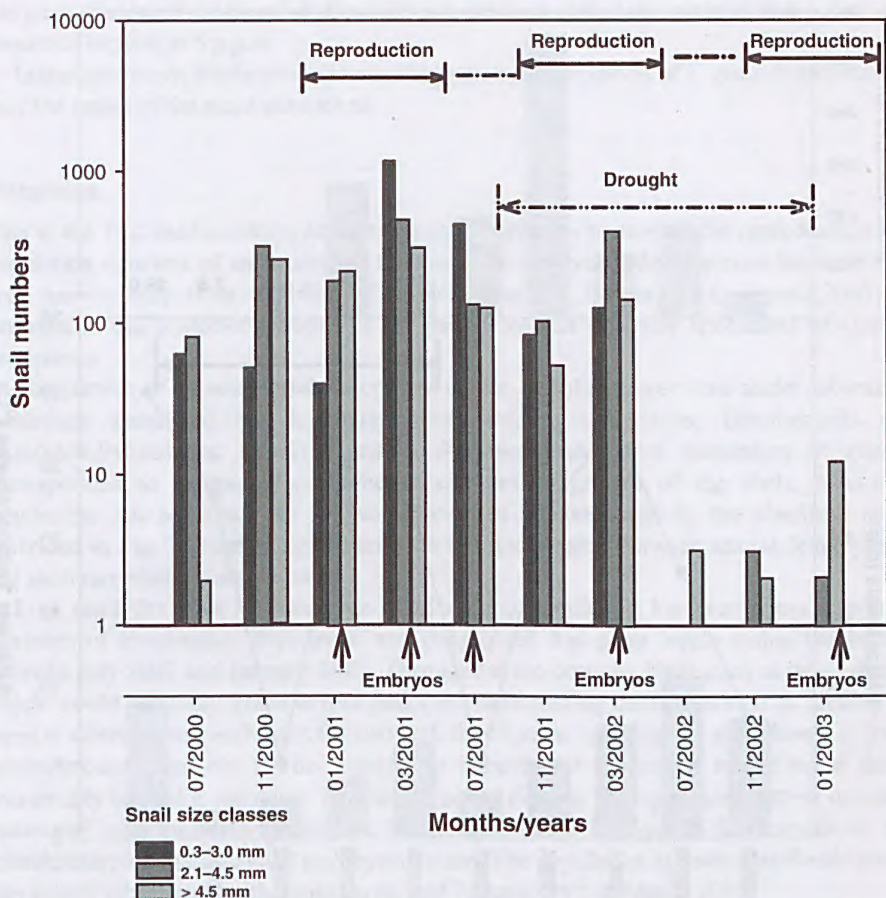
Fig. 3. Results of analyses of 4736 *Gabbia vertiginosa* collected from Saumarez Road swamp during quarterly surveys between July 2000 and January 2003 (*y*-axis log-transformed). Snails were divided into three shell-length classifications: 0.3–2.0 mm, 2.1–4.5 mm and >4.5 mm actual individual shell lengths. Approximate commencement of reproduction period was determined by date of first finding of freshly hatched snails in habitat (mean shell length at this stage: 0.25–0.3 mm) minus 30–34 days deposition to hatching period as determined in laboratory breeding trials. Approximate ending of reproduction period was determined by date of last finding of freshly hatched snails in habitat (mean shell length at this stage: 0.25–0.3 mm) minus 30–34 days.

conditions such as those that exist across the New England Tablelands (Bureau of Meteorology Australia 2001). The peak in size class 2.1–4.5 mm in March 2002 (a quarterly January 2002 survey was not done) suggests that embryos were deposited during the first weeks of January 2002 (72 days from deposition to mean shell size 3 mm; Fig. 2). The appearance of embryos in January, March and July of 2001 indicates that *G. vertiginosa* may be capable of reproducing more than once a year, if environmental conditions are favourable. Drought across the region caused a dramatic fall in snail densities from April 2002 onwards in response to reduced habitat, but some embryos were found in January 2003 indicating that reproductively viable adults still remained. Rainfall
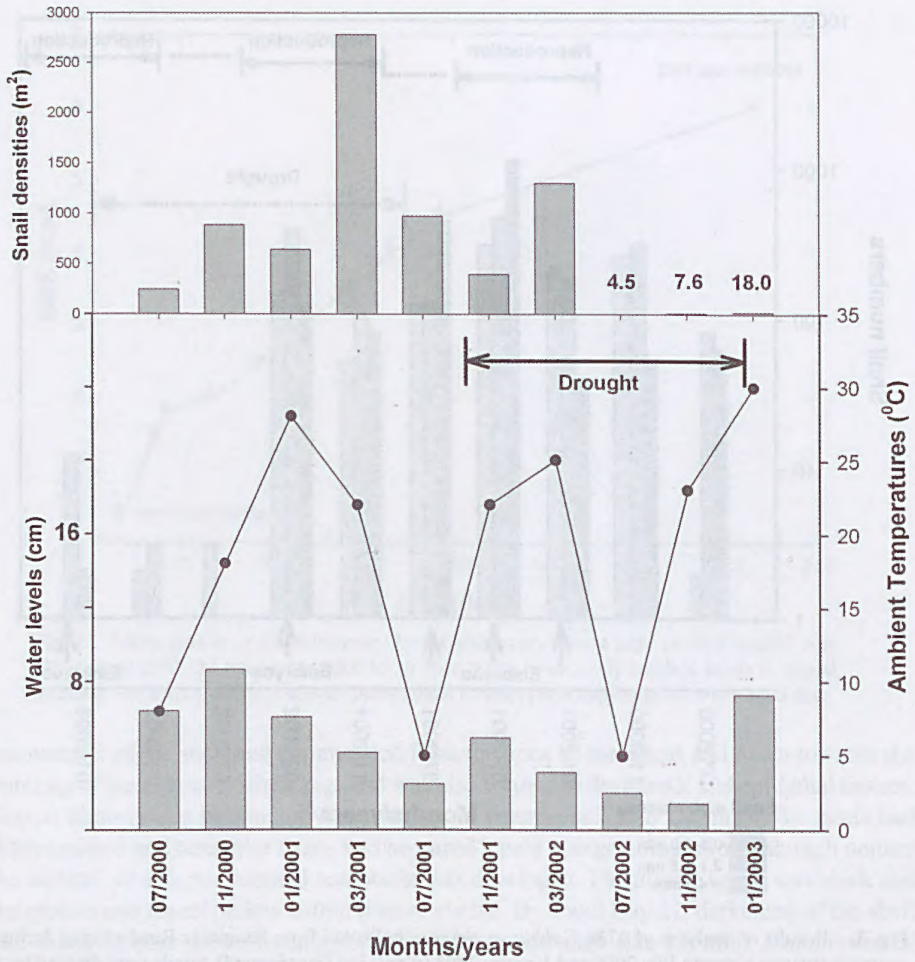
Fig. 4. Analyses of snail densities (upper panel) collected during each quarterly survey at Saumarez Road swamp between July 2000 and January 2003, in relation to habitat water levels (lower panel, bar graph) and ambient air temperatures at the site (lower panel, line graph).

across the New England Tablelands in January 2003 appears to have had a positive impact on snail reproduction leading to the small peak in juvenile numbers observed in March 2003.

Population densities for *G. vertiginosa* calculated at each quarterly survey at Saumarez Road swamp fluctuated with the changing of the seasons and dropped dramatically in the latter half of the drought period (Fig. 4). Densities were highest in March of each year, corresponding with the nearing of the end of summer. At this time, air and water temperatures averaged 23°C and habitat water levels were still high enough to support the growth of *E. gratioloides*, the latter apparently important to the survival, growth and reproduction of the snail. The severe drop in water levels in July and November 2002 reduced the coverage of *E. gratioloides* in the habitat from ≈ 2.5 m² to 0.2 m². Snail densities at these times were also at their lowest. Water quality tests conducted at the study

site gave consistent readings of about pH 8.0, calcium carbonate levels of 669 p.p.m. and dissolved oxygen at 5 p.p.m.

In the laboratory, snails were observed to graze upon the leaves of *E. gratioloides* leaving only the stalks of the plant untouched.

Discussion

This is the first medium-term study to provide a general picture of the reproduction and population structure of an Australian bithyniid. Its embryonic development has until now been known only from unpublished observations (W. Ponder, pers. comm. 2003) of embryos in the posterior sections of the pallial oviduct of a few specimens of *Gabbia vertiginosa*.

The pattern of growth and development of the hatchlings over time under laboratory conditions paralleled the Saumarez Road swamp collections. Eleutheriadis and Lazaridou-Dimitriadou (2001) found in *Bithynia graeca* that maturation of gonads corresponded to external morphometric changes in growth of the shell. A similar conclusion can be drawn for *G. vertiginosa*, as demonstrated by the size/time ratios described in Fig. 2. Further experiments on the relationship between sexual development and shell morphology are required.

Low snail densities at Saumarez Road swamp parallelled low water levels, greater extremes of temperature than usual and consequent low plant levels within the habitat between July 2002 and January 2003. Throughout the drought, birds such as wood ducks, which would normally graze across paddocks surrounding dams, resorted to feeding on weed in watercourses and dams for survival, thus further reducing the plant levels in those environments (pers. obs.). This significant behavioural adaptation in the wood ducks presumably caused a reduction in snail densities directly through consumption of snails associated with the water plants and indirectly through the loss of food resources and microhabitat for snail survival and reproduction. The population at Saumarez Road swamp was slowly rebuilding, with densities around 22 snails m^{-2} in March 2003.

From the present study, *G. vertiginosa* has been shown to be a hardy species with a high growth rate (88 days to 3.5 mm) compared with *Bithynia graeca*, an annual species that takes 210 days to grow to 3.5 mm (Eleutheriadis and Lazaridou-Dimitriadou 2001). The larger *B. tentaculata* can live up to 51 months but takes a full 2 years to reach sexual maturity (Vincent *et al.* 1981; Brendelberger 1995).

Gabbia vertiginosa is a fast-growing snail with a shorter life span than *B. tentaculata*. It reaches sexual maturity earlier and reproduces at least annually, although it is able to take advantage of favourable environmental cues to produce more than one recruitment cycle per annum.

Gabbia vertiginosa appears to be able to withstand harsh environmental conditions and has the ability to survive in habitats where the water is hard (669 p.p.m. calcium carbonate) and alkaline (pH 8.0) and with low dissolved oxygen levels (5 p.p.m.). In contrast, *Bithynia graeca* and *B. tentaculata* can tolerate only up to 110.3 p.p.m. carbonate and require ≈ 9.7 ppm dissolved oxygen for survival and reproduction (Lilly 1953; Eleutheriadis and Lazaridou-Dimitriadou 1995, 2001). Eleutheriadis and Lazaridou-Dimitriadou (2001) demonstrated that variation in pH, dissolved oxygen and carbonate hardness levels had detrimental effects on abundance, growth and reproduction of *B. gracea*. A similar controlled laboratory experiment with *G. vertiginosa* would benefit our present knowledge of the species' range of habitat parameters.

There is need for a more detailed and prolonged study of *G. vertiginosa*, both in natural habitats and under laboratory conditions, so that the biology and embryonic development of the species can be more fully understood under all conditions. Sampling with replacement of tagged snails would clearly define life span and reproductive patterns. A carefully planned laboratory breeding program is needed to describe the stages of embryonic development and provide information on the effects of environmental factors such as diet, pH, dissolved oxygen and temperature. Laboratory observations to date suggest that *G. vertiginosa* is not semelparous, in contrast to *B. graeca* and *B. tentaculata* (Calow 1978; Eleutheriadis and Lazaridou-Dimitriadou 2001), but further studies are required to build on the foundations of the profile of this species provided here.

Acknowledgments

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A protandric assimineid gastropod: *Rugapedia androgyna* n. gen. and n. sp. (Mollusca : Caenogastropoda : Rissooidea) from Queensland, Australia

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Abstract

A new genus and species of Assimineidae, *Rugapedia androgyna*, is described from mangrove swamps in Queensland, Australia. It differs from other assimineid genera in several anatomical and radular characters, including an anterior pedal mucous gland composed of elongate cells arranged in a transverse row (unique for the subfamily Assimineinae), and the sole of the foot has distinct transverse rugae, a trait which is unique for the family. This species is also shown to be the first case of protandry in the family.

Additional keywords: Assimineidae, Gastropoda, hermaphrodite, protandry, mangrove, anatomy, taxonomy.

Introduction

Assimineids occur worldwide in all temperate and tropical areas, with marine, estuarine, freshwater and terrestrial taxa. Members of the family are common in estuarine habitats in many parts of Australia, but the Australian fauna has never previously been revised. Fukuda and Ponder (2003) reviewed the family and genus-group names attributed to the Assimineidae. Many of these taxa are poorly known, in some cases only from shells. Nevertheless, their review makes it possible to allocate genera and recognise new taxa with reasonable certainty.

This paper represents one of a series describing the temperate and subtropical Australian taxa. During this work a new species that could not be placed in any of the existing genera was investigated and found to be protandric.

Materials and methods

Specimens used in this study are mostly housed in the Australian Museum (AMS) with paratypes lodged in the Queensland Museum (QM) and the Laboratory of Conservation of Aquatic Biodiversity, Faculty of Agriculture, Okayama University (OKCAB). Dissected specimens were fixed in ~10% formalin and stored in 7% seawater formalin.

Specimens were measured using a digitising pad as described by Ponder *et al.* (1989). The shells of a subset of these specimens were then removed and the animals sexed. The remaining unsexed specimens were retained as vouchers.

Dissections were carried out using a Leica stereoscopic microscope using a drawing apparatus. Radulae, opercula and shells were examined using a Leo 435 VP scanning electron microscope and were mounted using standard techniques.

The graph of sex and shell size was generated using SYSTAT ver. 7 (SPSS Inc., Chicago, IL, USA).

Systematics

Rugapedia n. gen.

Type species: *Rugapedia androgyna* n. sp.

Diagnosis

Shell solid, opaque, conical; protoconch consisting of protoconch I and II with indistinct thread below suture; teleoconch whorls slightly convex, sutures weakly impressed, with distinct subsutural spiral cord, otherwise smooth except for fine collabral growth lines; colour uniform dark brown; aperture pyriform with thin outer lip and thick, wide columellar lip; no varix, outer lip prosocline (~30°); lower base with spiral ridge surrounding umbilical area; umbilicus closed or with narrow chink. Operculum simple, pyriform, paucispiral, horny, translucent. Head–foot with no cephalic tentacles, with distinct omniphoric groove; anterior pedal mucous gland composed of several elongate, white cells arranged in transverse row just behind slit; sole slender when foot extended; propodium flat, smooth; metapodium usually shows many distinct regularly spaced wrinkles visible when extended or contracted. Radula taenioglossate; central teeth with no basal cusps; lateral teeth rectangular; inner marginal teeth long, slender; outer marginal teeth extremely wide, triangular, fan-shaped, with many tiny cusps but no secondary cusps. Prostate gland simple, slender; penis simple, large, with weak keel on outer edge of middle portion and distal end with short, narrow papilla with opening at tip. Coiled (renal) oviduct with one loop; seminal receptacle large, oval, colourless except for iridescent contents; arises from oviduct slightly anterior to end of coiled oviduct and lies between anterior end of bursa copulatrix and posterior end of albumen gland; bursa copulatrix large, elongately triangular, posterior to albumen gland; bursal duct long, straight; arises from oviduct at point where oviduct enters albumen gland; opens to anterior portion of bursa at ventral edge; pallial oviduct long, runs nearly straight to opening of pallial cavity; albumen gland white, opaque; capsule gland with three glandular zones; sperm duct completely surrounded by glandular pallial oviduct within central region of oviduct; vestibule narrow, muscular, with genital opening at anterior end. Right pleural and supraoesophageal ganglia separated from each other by long pleural-supraoesophageal connective; left pleural ganglion completely fused with suboesophageal ganglion.

Remarks

Anatomically, *Rugapedia* resembles *Aviassiminea* (Fukuda & Ponder, 2003) in most of the features of the pallial cavity, alimentary canal (other than the radula) and nervous system. However, the reproductive system differs in several details. There are no other published detailed anatomical studies of other genera of Assimineinae (see Fukuda and Ponder 2003 for a summary of known information).

Rugapedia has no basal cusps on the central teeth of the radula and lacks cephalic tentacles. This combination of characters is known in nine valid genera of the Assimineidae listed under Group 2 *sensu* Fukuda and Ponder (2003). Basal cusps are absent in a few additional genera for which the head-characters are unknown. A few of these resemble Group 2 taxa rather than Omphalotropidinae (Group 3). The genera without basal cusps and those in Group 2 can be divided up according to characters of the shell and operculum as follows:

Key to genera of Assimininae lacking basal cusps on the central teeth of the radula

1. Operculum with calcareous layer on outer side . . . . *Metassiminea* Thiele, 1927
   Operculum horny, simple 2
2. Shell with spiral ridge on base . . . .
   . . . .*Cyclotropis* Tapparone-Canefri, 1883; *Taiwanassiminea* Kuroda & Habe, 1950
   Shell with no spiral ridge on base 3
3. Umbilicus absent . . . . *Optediceros* Leith, 1853; *Paludinella* Pfeiffer, 1841;
   . . . .*Leucostele* Thiele, 1927; *Pseudassiminea* Thiele, 1927
   Umbilicus present 4
4. Translucent, fragile colourless shell. . . . . *Acmella* Blandford, 1869; *Cavernacmella* Habe, 1942
   Opaque, brown, strong shell . . . . *Ekadanta* Rao, 1928; *Solenomphala* Heude, 1882

Among these genera, *Cyclotropis* and *Taiwanassiminea* are the most similar to the new genus in being based on species having both a distinct basal ridge and a spiral cord or groove just below the suture. *Cyclotropis* differs from *Rugapedia* in radular characters, the central teeth being much shorter and wider (van Benthem Jutting 1963; Brandt 1974; Fukuda and Ponder in press) and in having a much larger, distinctly umbilicate shell. *Taiwanassiminea* also has short central teeth with a narrow thickening on the lateral edges and the shell has a spiral cord or groove on the periphery, but this is located just above the suture (Habe 1942; Pace 1973; Fukuda and Mitoki 1996*a*) not below it in the type species. However, other taxa included in *Taiwanassiminea* (Fukuda and Ponder in press) have the spiral cord below the suture and lack a peripheral cord or groove. There are several other important differences between *Taiwanassiminea* and *Rugapedia* including the former genus having a simple sole and the capsule gland consisting of a single glandular mass, not three distinct zones (Fukuda and Ponder in press).

The radula of *Rugapedia* is unique and the combination of tooth shape seen in this genus has not been reported in other assimineids. The fan-shaped wide outer marginal teeth with a simple row of cusps are also known in *Solenomphala* and several genera listed as Group 3 (= subfamily Omphalotropidinae) by Fukuda and Ponder (2003). However, members of this group have cephalic tentacles (e.g. *Allepithema* Tomlin, 1930; *Ditropisena* Iredale, 1933; *Paludinellassiminea* Habe, 1994). The radula of *Ditropisena* (H. Fukuda, personal observation) is most similar to that of *Rugapedia* but differs in the expansion of the ventral region of the central teeth in the new genus. Moreover, *Ditropisena* has a depressed trochiform shell with strong spiral and axial ribs and a wide umbilicus, as well as a circular operculum with a central nucleus and long cephalic tentacles (Fukuda and Ponder 2003).

The head–foot of *Rugapedia* is unique in having numerous transverse rugae on the sole of the foot that persist even in fixed material. This character is unknown in any other assimineid and may even be unique within the Rissooidea. It also has multiple glandular sacs opening to the anterior edge of the foot, another character not seen in any other Assimineinae but known in a few Omphalotropidinae (H. Fukuda, personal observation).

Because anatomical studies are few, we cannot compare the anatomical characters of *Rugapedia* with most of the assimineine genera listed by Fukuda and Ponder (2003). One Australian species of *Taiwanassiminea* (Fukuda and Ponder in press) differs from *Rugapedia* in having the vestibule arising from the mid-ventral portion of the capsule gland but we do not know if this is typical of that genus. General arrangements of the reproductive and nervous systems of *Rugapedia* are generally similar to those of *Assiminea* Fleming, 1828, a genus of Fukuda and Ponder's (2003) Group 1 (= subfamily Assimineinae; cephalic tentacles absent, central teeth of the radula with basal cusps), but the type species of *Assiminea* has a strongly coiled anterior vas deferens around the prostate gland, a

longitudinal row of distinct papillae on the penis, and a black seminal receptacle (Fukuda and Ponder unpublished observations).

Although the species described below is a protandrous hermaphrodite, two others that appear to be congeneric are dioecious, one from Queensland and one from Okinawa. These will be described elsewhere.

Etymology

Ruga (Latin): wrinkle; *pedis* (Latin): foot.

Rugapedia androgyna n. sp.

(Figs 1–4)

Material examined

Holotype. Tooan Tooan Creek, Hervey Bay, QLD, 25°17'S, 152°50.683′E, upper shore among dead leaves on sand in mangroves, W. F. Ponder & H. Fukuda, 3 Mar. 2003 (AMS C.429858).
Paratypes. **Queensland**: same locality as holotype (AMS C.429527, 8 wet specimens: 4 complete shells and 4 bodies); South Trees Inlet, SE of Gladstone, 23°57.833′S, 151°20.250′E, mangrove swamp, 8 Sep. 2003, H. Fukuda & J. Studdert (AMS C.429092, 69 wet: 49 shells, 20 bodies, 8 dry, 1 on s.e.m. stub; QM MO64286, 3 wet; OKCAB M5424, 5 wet; AMS C.429859, 1 dry specimen, figured); Toolara, Tin Can Bay, 25°55.400′S, 153°0.483′E, upper shore, mangrove swamp, 4 Mar. 2003, W. F. Ponder & H. Fukuda (AMS C.429528, 7 wet specimens: 2 shells and 5 bodies; AMS C.429529, 1 dry specimen, figured); NE of Gympie, Tin Can Bay, 25°57'S, 153°0'E, small mangrove creek, under bark on dead roots, 22 Oct. 1976, I. Loch (AMS C.414899, 4 shells, 1 body).
Other material examined. **Queensland**: Gladstone, 23°51'S, 151°16'E, 1904 (AMS C.018798, 12 shells); 0.5 km S of Urangan Boat Anchorage, Hervey Bay, 25°19'S, 152°54'E, under leaves and wood in pools in mangroves, 24 Oct. 1976, I. Loch & B. Duckworth (AMS C.416547, 2); Pine River, N of Brisbane, 27°52.5'S, 153°0'E, under bark of rotting log, 1975, J. McNalty (AMS C.414866, 12).

Description

Shell (Fig. 1) small, ovate-conic to conic (Fig. 1*A–C*), thick, opaque. Protoconch (Fig. 1*D, E*) of ~2.1–2.2 weakly convex whorls, with smooth surface except for spiral cord below suture (Fig. 1*G*). Teleoconch uniform dark chestnut brown, of up to about four weakly convex whorls, sculptured with weak collabral growth lines; suture shallow, weakly impressed; distinct subsutural spiral keel (becomes groove if eroded, as observed in species of *Angustassiminea* Habe, 1943 by Fukuda and Mitoki (1996*b*)) below suture. Aperture wide, pyriform; peristome complete, sharp, with no apertural varix; outer lip prosocline, not expanded; parietal lip narrow, rather long, slightly curved, thin, transparent; columellar lip thick, wide, distinctly curved, anterior end forming strong projection crossing anterior part of outer lip, forming shallow canal. Umbilicus narrow chink or closed; umbilical area surrounded by strong spiral ridge (Fig. 1*F*). Dimensions (Table 1).

Operculum (Fig. 2*A, B*) pyriform, paucispiral, with last whorl very large; horny, thin, flat, yellowish, transparent, simple on inner surface; muscle scar elongate, occupying ~2/3 of length of columellar side of inner surface.

Head–foot (Fig. 3*A–E*). Majority of head–foot covered with dense (less well developed in some specimens) black pigment in many specimens (Fig. 3*A, B*), except for colourless, translucent eye lobe, anterior end of snout (in some specimens), sole, omniphoric groove and opercular lobe. Triangular eye lobes (el, Fig. 3*B*) each with conspicuous, black eye at middle and crescent-shaped black pigmentation spot at tip. Cephalic tentacles absent. Snout long, bilobed. Foot large, wide, anterior and posterior ends simple and rounded. Opening to anterior mucous gland (Fig. 3*E*) wide, transverse slit just
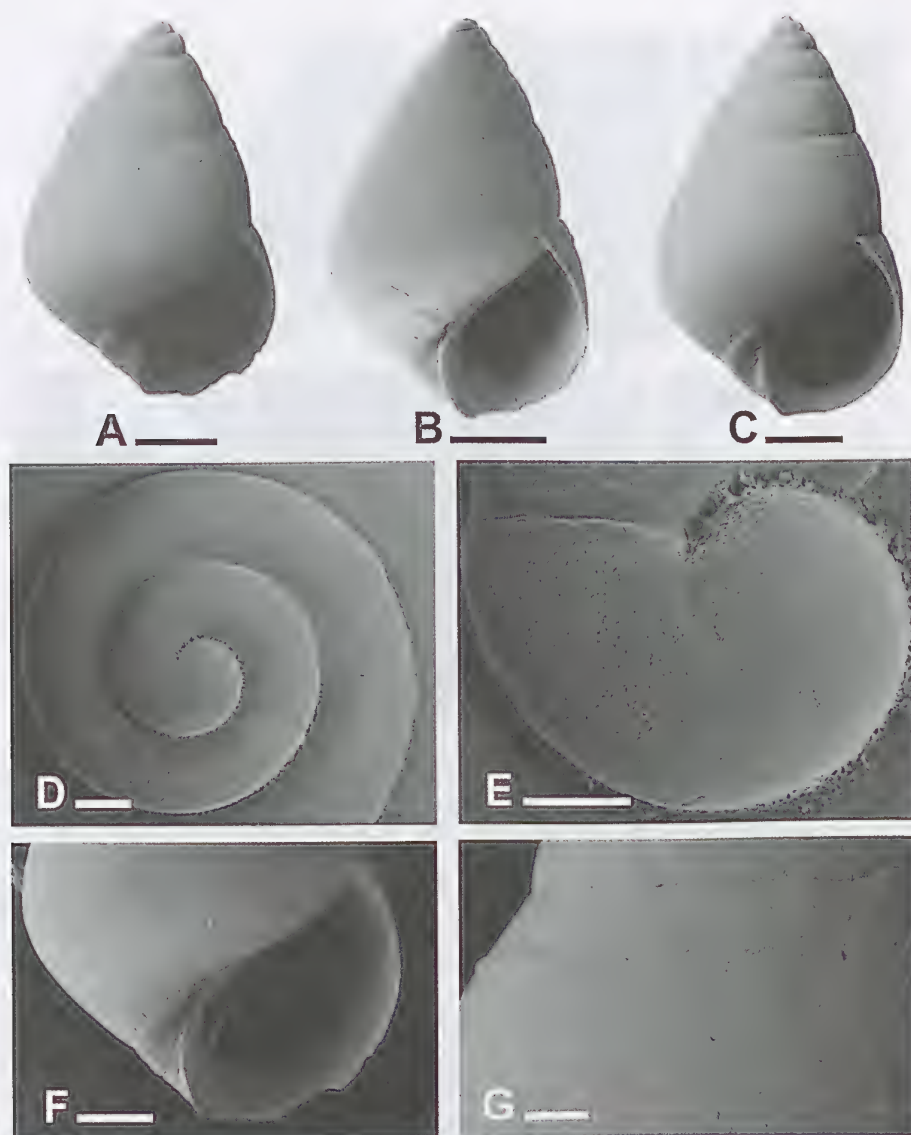
Fig. 1. *Rugapedia androgyna* n. sp. *A–C*, shell: *A*, holotype, Tooan Tooan Ck, Hervey Bay, Qld (AMS C.429858); *B*, paratype, Toolara, Tin Can Bay, Qld (AMS C.429529); *C*, South Trees inlet, SE of Gladstone, Qld (AMS C.429092); *D–G*, details of shell of holotype: *D, E*, protoconch; *F*, detail of base; *G*, suture area on last whorl, showing subsutural thread. Scale bars: *A–C*, 500 µm, *D*, 50 µm, *E*, 30 µm, *F*, 300 µm, *G*, 100 µm.

posterior to anterior end of foot; posterior lip of slit usually bent backward when animal alive. Anterior pedal mucous gland (apg, Fig. 3*D, E*) composed of several elongate, white cells (Fig. 3*E, F*), each with two or three tiny ducts visible through translucent sole epithelium; mucous cells arranged in transverse row just behind slit. No posterior pedal mucous gland or metapodial tentacle present. Wide omniphoric grooves (og, Fig. 3*A*) run ventrally on both sides of head; right groove wider than left. Right groove carries faecal

Table 1. Shell dimensions of *Rugapedia androgyna* n. sp.
Number of specimens given in brackets after the registration number. Ranges: minimum–maximum (mean) ± standard deviation (mm).

	Shell length	Shell width	Aperture length	Aperture width	Length of last whorl	Total whorls
Holotype	2.37	1.64	1.08	0.88	1.77	5.6
Figured specimens						
(C.429529)	2.37	1.58	1.15	0.93	1.73	5.9
(C.429092)	2.78	1.70	1.24	1.02	1.91	6.1
Paratypes C.429528 (8)	1.29–1.56 (1.86) ± 0.47	0.99–1.65 (1.31) ± 0.27	0.66–1.06 (0.85) ± 0.14	0.52–0.96 (0.76) ± 0.14	0.98–1.88 (1.37) ± 0.32	4.4–5.8 (5.0) ± 0.51
Paratypes C.414899 (9)	2.06–3.01 (2.64) ± 0.36	1.37–1.99 (1.76) ± 0.22	0.86–1.45 (1.20) ± 0.19	0.79–1.13 (1.01) ± 0.12	1.50 2.21 (1.95) ± 0.25	5.1–6.0 (5.6) ± 0.31
C.414866 (13)	1.64–3.09 (2.53) ± 0.38	1.21–2.00 (1.74) ± 0.22	0.77–1.33 (1.11) ± 0.17	0.75–1.15 (1.00) ± 0.11	1.30–2.28 (1.91) ± 0.27	4.3–5.4 (5.1) ± 0.29
C.416547 (2)	2.89, 2.91	1.88, 1.93	1.29, 1.30	1.05, 1.11	2.02, 2.11	5.4, 6.0
C.18798 (7)	1.97–2.81 (2.44) ± 0.33	1.36- 1.74 (1.55) ± 0.16	0.90–1.21 (1.09) ± 0.12	0.79–1.06 (0.92) ± 0.10	1.39–1.89 (1.70) ± 0.19	5.5–6.1 (5.9) ± 0.23
C.429527 (10)	1.49 2.40 (1.93) ± 0.36	1.04–1.64 (1.34) ± 0.24	0.71–1.10 (0.89) ± 0.15	0.63–0.89 (0.77) ± 0.10	1.14–1.78 (1.49) ± 0.25	4.7–5.8 (5.3) ± 0.36
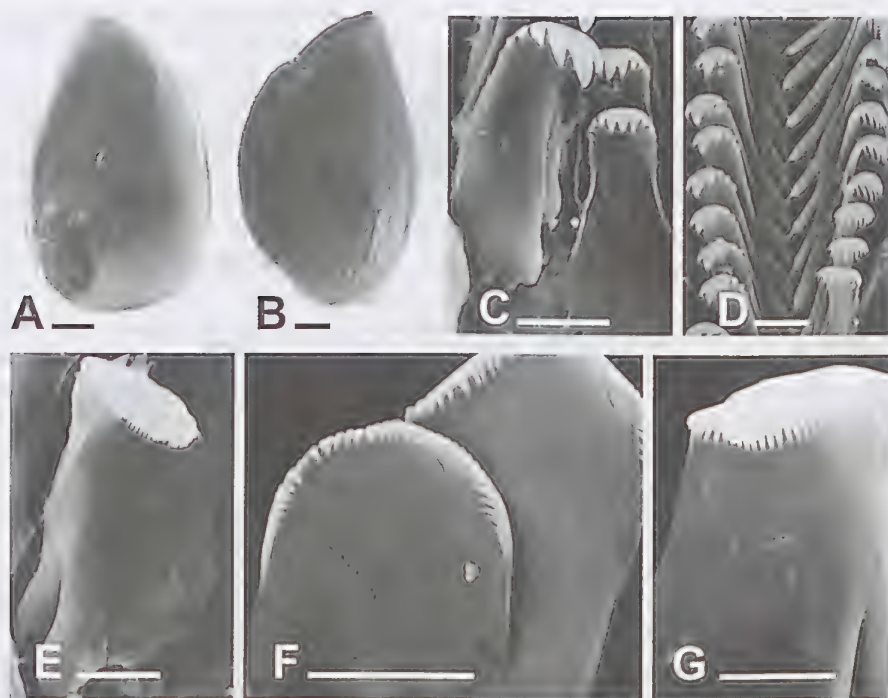
Fig. 2. *Rugapedia androgyna* n. sp. *A, B*, opercula: *A*, outer side; *B*, inner side, from paratypes, Tooan Tooan Creek, Hervey Bay, Qld (AMS C.429527). *C–G*, radula: *C–E, G*, Tin Can Bay, Qld (AMS C.414899); *F*, paratype, Toolara, Tin Can Bay (AMS C.429528); *C*, central and lateral teeth; *D*, lateral and inner marginal teeth; *E–G*, outer marginal teeth. Scale bars: *A, B*, 100 μm, *C–G*, 10 μm.

pellets from inside pallial cavity to exterior. Sole (Fig. 3*C*, *D*) slender when foot extended; propodium flat, smooth; metapodium usually shows ~20 distinct regularly spaced wrinkles visible when extended or contracted. Mode of locomotion 'step-like'.

Pallial cavity. Pallial cavity large, spacious, occupies about two thirds of last whorl. Pallial roof with black pigmentation, particularly in dorsal half and anterior mantle roof. Kidney opening conspicuous, in posterior-most corner of cavity; kidney entirely behind pallial cavity, compact, consisting of mass of colourless, transparent cells. Gill rudimentary, a row of four blunt, finger-like filaments consisting of only gf1 (inner side of filament; see Fukuda and Ponder 2003); on posterior portion of efferent vein on left side of cavity. Osphradium similar to *Aviassiminea* (Fukuda and Ponder 2003: fig. 4*A*), small, elongate-oval, containing conspicuous osphradial ganglion. Hypobranchial gland absent.

Digestive system. Mouth opens between pair of muscular lips into buccal cavity. Buccal mass large, wide, occupying most of snout. Radula (Fig. 2*C–G*) taenioglossate; central teeth (Fig. 2*C*) spatula-shaped, much longer than wide; with 11–14 long, triangular cusps on cutting edge; three middle cusps longer than lateral ones, median cusp not markedly larger than pair of adjacent cusps; no basal cusps; lateral edges slightly thickened in upper two thirds, unthickened ventrally, nearly straight and parallel for about one third of length, then gently splayed; ventral region about twice as wide as cutting edge; base convex, simple, with no basal tongue. Lateral teeth (Fig. 2*C*, *D*) slightly longer than central teeth, rectangular, with no cusp on face of tooth; cutting edge with pointed median cusp
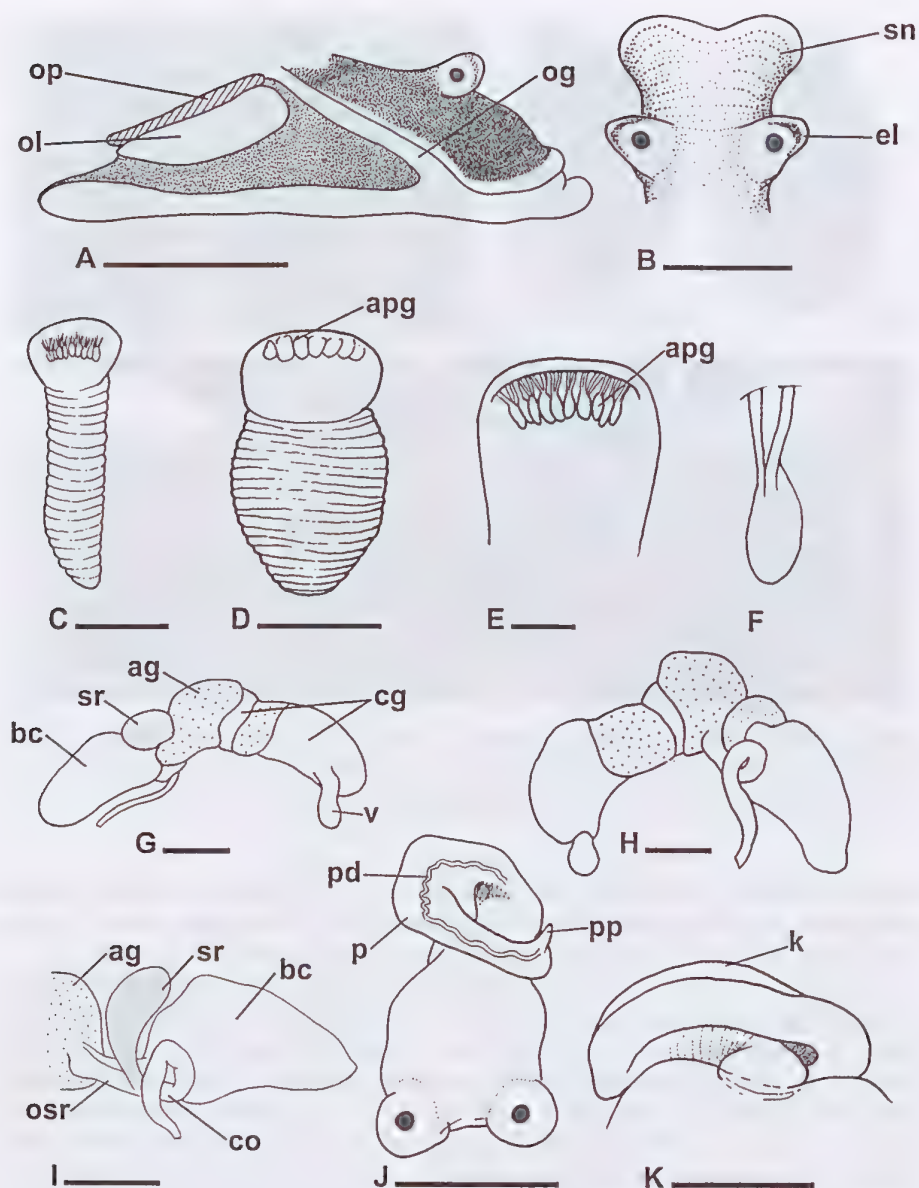
Fig. 3. *Rugapedia androgyna* n. sp., Tooan Tooan Creek, Hervey Bay, Qld (AMS C.429527). *A*, head–foot from right side; *B*, dorsal view of head; *C, D*, sole of foot, *C*, extended, *D*, contracted; *E*, schematic dorsal view of anterior end of foot showing detail of anterior pedal mucous gland; *F*, detail of one of pedal mucous gland elements; *G–I*, female reproductive system, *G*, view from right side, *H*, view from left side, *I*, detail of sperm sacs and coiled oviduct from left side; *J*, dorsal view of head and penis; *K*, lateral view of penis. Scale bars: *A–D, J*, 500 μm; *E, K*, 250 μm; *G, H*, 150 μm; *I*, 200 μm. Key to abbreviations: ag, albumen gland; apg, anterior pedal mucous gland; bc, bursa copulatrix; cg, capsule gland; co, coiled oviduct; el, eye lobe; k, keel (on penis); og, omniphoric groove; ol, opercular lobe; op, operculum; osr, oviduct anterior to seminal receptacle; p, penis; pd, penial duct; pp, penial papilla; sn, snout; sr, seminal receptacle; v, vestibule.

(about twice as long as adjacent cusps) and 3–4 pairs of smaller cusps on outer edge, one on inner edge; moderately long, oblique accessory plates at outer side of lateral teeth (Fig. 2D). Inner marginal teeth (Fig. 2D) long (about twice as long as central teeth), slender, gently curved, with parallel sides, cutting edge with 8–10 long, sharp cusps; base simple, rounded. Outer marginal teeth (Fig. 2E–G) extremely wide, triangular, fan-shaped, expanded in distal region; with more than 20 simple, tiny, sharp cusps on broad cutting edge; no secondary cusps; inner lateral edge thickened; base simple. Oesophagus opens widely to buccal cavity. Pair of glandular, black buccal pouches at posterior-most corner of dorso-lateral sides of buccal mass. Salivary glands short, simple, club-like, with black pigmentation, located at dorso-lateral sides of buccal mass, not passing through nerve ring. Oesophagus simple; enters stomach on left side at junction of anterior and posterior chambers. Stomach with single opening to digestive gland posterior to oesophageal opening. Digestive gland pale lemon-yellow; composed of two parts; anterior portion mass of small cells covering part of anterior and posterior stomach, posterior part two rows of large, finger-like lobes in upper whorls of visceral coil; lobes of outer row longer than those of inner rows. Style sac large, with crystalline style, bean-shaped. Origin of intestine at right anterior end of anterior chamber of stomach. Intestine tightly looped over anterior tip of style sac before continuing to rectum; rectum forms conspicuous S-shaped coil in middle of pallial roof. Oval faecal pellets queued in single file in intestine and rectum. Anus simple, situated slightly posterior to anterior mantle edge.

Male reproductive system. Testis large, bright orange, consisting of 6–10 bundles of wide lobes. Coiled seminal, tubular vesicle arises from vas efferens in antero-ventral region of digestive gland; wide, highly convoluted. Posterior vas deferens runs from seminal vesicle as straight tube crossing over oesophagus and running to middle part of prostate gland just within pallial cavity. Prostate gland slender, whole gland equal to about half length of pallial cavity. Anterior vas deferens arises from middle part of prostate gland close to entry point of posterior vas deferens, passes straight across pallial roof and enters muscular wall of neck, nearly straight before reaching proximal end of penis. Penis (Fig. 3J, K) large, muscular, on right side of head; forming anticlockwise coil when at rest; simple, tapering; with weak keel (k, Fig. 3K) on outer edge of middle portion; penial duct weakly undulating within penis; located in middle; distal end with short, narrow papilla (pp, Fig. 3J) with opening at tip. Transitional male with penial scar (absent in mature females).

Female reproductive system (Fig. 3G–I). Ovary simple sac with many white cells, covering ventro-lateral area of digestive gland. Posterior oviduct convoluted slightly, runs along oesophagus, on right lateral edge. Coiled (renal) oviduct (co) with one loop. Seminal receptacle (sr) large, oval, long, lacks distinct duct, colourless except for iridescent contents; arises from oviduct slightly anterior to end of coiled oviduct and lies between anterior end of bursa copulatrix and posterior end of albumen gland, distal half visible on right side of oviduct. Oviduct anterior to seminal receptacle (osr) of moderate length, straight, with small pocket just posterior to point where it enters left ventro-posterior end of albumen gland. Bursa copulatrix (bc) large, elongately triangular, posterior to albumen gland. Bursal duct long, straight; arises from oviduct at point where oviduct enters albumen gland; opens to anterior portion of bursa at ventral edge. Pallial oviduct long, runs nearly straight to opening of pallial cavity; clearly divided (in dissection) into albumen gland posteriorly and capsule gland anteriorly. Albumen gland (ag) white, opaque. Capsule gland (cg) with three glandular zones; anterior and (short) posterior ones translucent; middle one opaque, similar in appearance to albumen gland. Sperm duct muscular, completely surrounded by glandular pallial oviduct and fused with lumen of oviduct (= median egg

channel) within central region of oviduct. Narrow muscular vestibule (v) extends beyond anterior end of capsule gland, genital opening at anterior end.

Nervous system. Not examined in detail. Each cerebral ganglion large, rather slender. Cerebral commissure as long as cerebral ganglion. Right pleural and supraoesophageal ganglia separated from each other by long pleural-supraoesophageal connective. Left pleural ganglion completely fused with suboesophageal ganglion. Each pedal ganglion moderate in size, separated by a short, distinct commissure.

Distribution and habitat

Known from Gladstone to Brisbane in southern Queensland (Fig. 4). Amongst leaves in wet areas in back part of mangroves.

Remarks

Given the scant sampling for small gastropods in mangrove habitats in Queensland, this species may well have a larger range than indicated by the available material. It is found living together with '*Assiminea*' *buccinoides* (Quoy and Gaimard, 1834), '*A.*' *tasmanica* Tenison-Woods, 1876, and '*A.*' ·n. sp. (Fukuda and Ponder in press), and can be distinguished from these species by its uniformly dark brown shell and the presence of a basal ridge. Another superficially similar species of assimineid included in *Taiwanassiminea* (see above) is found in the upper parts of large estuaries from at least Rockhampton to the Shoalhaven River. This has a prominent basal ridge but differs in having a larger, banded shell as well as in radular and anatomical characters (Fukuda and Ponder unpublished observations).
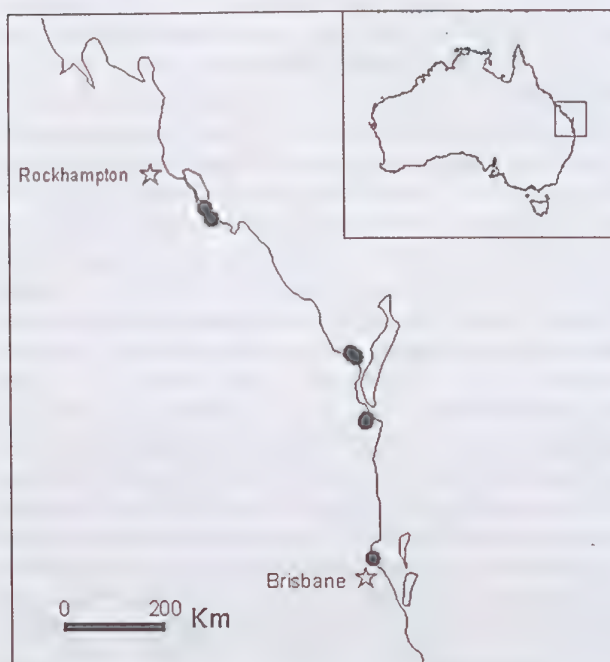
Fig. 4.   Distribution of *Rugapedia androgyna* n. sp.

As mentioned above, at least two similar species are known, one from Queensland and the other from Okinawa. Preliminary investigation of these samples indicates that these species are both dioecious. Thus, if they are congeneric, protandry is not a generic character.

Etymology

Androgynus (Latin): hermaphrodite.

Sex change

The available samples contained only a few juveniles. These were all investigated and the results are summarised in Tables 2 and 3 and in Fig. 5.

Mature males are small and have a large penis. One transitional specimen was observed with a detached penis lying in the mantle cavity, and a scar was visible on the head where the penial base was attached. The scar is absent in mature females. This observation suggests the possibility that the penis is detached and shed rather than being absorbed during the transition from male to female.

Discussion

Small gastropods in mangrove habitats have been very poorly collected let alone studied in Queensland, an observation reinforced by the discovery of this unusual assimineid in what amounts to little more than casual collecting.

The great majority of caenogastropods are dioecious, with only a very few known to be protandric hermaphrodites (Webber 1977; Hoagland 1978; Wright 1988; Fretter and Graham 1994). By far the best known are the calyptraeids (e.g. Fretter and Graham 1994;
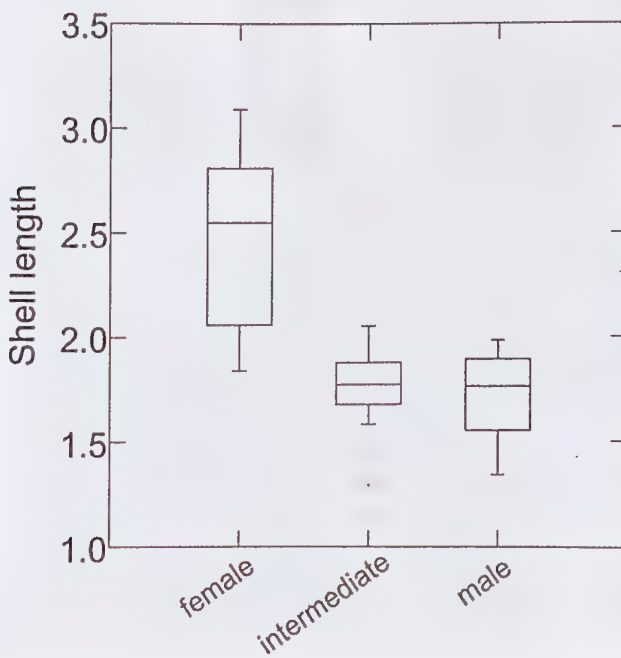
Fig. 5. Box plot of shell lengths and sex of *Rugapedia androgyna* n. sp. The horizontal line represents the median value; the limits of the box mark the first and third quartiles (i.e. the central 50% of values fall within the box. The whiskers represent the range of values that fall within 1.5 H spreads of the hinges (see SYSTAT *v.* 7 Graphics manual). The asterix represents an outlying value.

Table 2. Sex of individual specimens

Specimen lot	Shell length (mm)	Gonad (and seminal vesicle)	Penis	Prostate	Bursa	Pallial oviduct	Sex
C.429092	1.6, 1.8, 1.9, 1.9, 1.9, 2.0	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.8, 1.8, 1.8, 2.1	Small ovary	Absent	Absent	Small	Small	Intermediate
	2.0	Large ovary	Absent	Absent	Small	Small	Intermediate
	1.8, 1.9, 2.0, 2.3, 2.3, 2.6, 2.8, 2.8, 2.9	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
C.429520	1.3, 1.4	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.9, 1.9	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
	1.3	Small ovary	Shed	Absent	Small	Small	Intermediate
C.414899	2.7, 2.8, 2.9, 3.0	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
C.429527	1.6	Large testis and seminal vesicle	Large	Large	Absent	Absent	Male
	1.6	Large testis and seminal vesicle	Large	Absent	Small	Small	Intermediate
C.414866	2.1, 2.1	Large ovary	Absent	Absent	Fully developed	Fully developed	Female
	2.5, 2.6, 2.6, 3.1	Large ovary	Absent	Absent	Fully developed	Fully developed	Female

Table 3. Size ranges of shell lengths of sexed specimens

Sex (no. specimens)	Size: minimum–maximum (mm) (mean)
Males (9)	1.34–1.98 (1.70)
Intermediate (7)	1.29–2.05 (1.74)
Females (21)	1.84–3.09 (2.45)

Collin 1995; Warner *et al.* 1996; Chaparro *et al.* 2001). Eulimids show a variety of strategies, including protandry (Hoagland 1978; Ponder and Gooding 1978; Warén 1983). Other examples include the cerithioidean *Vermicularia* (Bieler and Hadfield 1990), the littorinid *Mainwaringia* (Reid 1986), the pelagic ptenoglossan *Janthina* (Laursen 1953; Graham 1954) and the coral-inhabiting neogastropod *Coralliophila violacea* (Soong and Chen 1991). Houbrick (1981, 1989) suggested the possibility of protandry in *Campanile* but this has not been demonstrated with certainty.

All other studied assimineids are dioecious with the exception of possible parthenogenesis reported in one African taxon *Pseudogibbula* Dautzenberg, 1891 (Brown 1980, 1994). The discovery of protandry in an assimineid is therefore surprising, especially as there has only been one other case reported within the very large and diverse superfamily Rissooidea: in a North American vitrinellid, which also appears to detach its penis before becoming female (Bieler and Mikkelsen 1988).

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A new species of *Lortiella* (Mollusca : Bivalvia : Unionoidea : Hyriidae) from northern Australia

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Abstract

A new species of *Lortiella*, *L. opertanea* n. sp., is described from the Katherine, Daly and Douglas Rivers, Northern Territory, and disjunctly in the Carson and King Edward Rivers of Western Australia. It appears to be the sister taxon to the allopatric *Lortiella rugata* (Sowerby, 1868), the type species of the genus, which occurs in drainages between the two sets of disjunct populations. Some notes on the anatomy of the genus are provided and the subfamily Lortiellinae Iredale, 1934 is synonymised with Velesunioninae.

Introduction

The Australian freshwater mussels (Hyriidae) were last revised by McMichael and Hiscock (1958) (as Mutelidae) and almost no changes to the systematics of the group have occurred since that time. They recognised *Lortiella* as a distinct genus within its own subfamily (Lortiellinae), which contained two species. *Lortiella* is the least known Australian hyriid genus, with little known of its anatomy or larvae, the only basis for the subfamily being the unusual elongate shell. McMichael and Hiscock (1958) suggest this genus has its closest relationships outside Australia, namely with the Asian genus *Solenaia* Conrad, 1869. Although this hypothesis has not yet been tested properly, *Solenaia* has a pallial sinus (which *Lortiella* lacks) and is included in the Unionidae (Unioninae) by Haas (1969a, 1969b). Hiscock in McMichael (1967) stated 'Preserved *Lortiella* recently studied by Dr I. D. Hiscock appear to be very similar in gross anatomy to the Velesunioninae' and Bonetto *et al.* (1987) also discussed this genus briefly. Walker *et al.* (2001) figured the glochidial larva of *Lortiella froggatti* and repeated McMichael and Hiscock's (1958) suggestion that the subfamilies Lortiellinae and Hyridellinae were derived from the Velesunioninae.

Considerable collecting of freshwater molluscs has occurred in northern Australia in the last 30 years and this additional material has resulted in more collections of *Lortiella* being available. Two specimens from the Katherine River were considered to be *L. rugata* by McMichael and Hiscock (1958) but the availability of more material shows specimens from this area represent a third species of *Lortiella*. In addition to describing this taxon, we add some observations on the gross anatomy of the genus and additional morphometric, locality and habitat data.

Materials and methods

Shell measurements

Shells were measured to the nearest 0.05 mm using manual calipers. The following dimensions are the same as those used by McMichael and Hiscock (1958: fig. 2): TL, total (i.e. maximum) length as measured from anterior margin to posterior margin; MH, maximum height measured from dorsal margin to ventral margin; BH, height at beak measured from beak to ventral margin at 180° from beak; W, inflation (width) measured

by a single valve held against calipers at ventral and dorsal margin and at greatest width created by posterior ridge (in specimens with two joined valves, the greatest width at the posterior ridge was measured and then divided by two); BL, length of beak measured from umbo to anterior end of shell along dorsal margin (differs from McMichael and Hiscock measurement that was at right angles to the vertical axis of the shell). All dimensions given are in mm. Ratios: MH/TL (= MHI of McMichael and Hiscock); BH/MH (= BHI of McMichael and Hiscock); W/TL; BL/TL (= BLI of McMichael and Hiscock); BH/ML.

For dry material, all available valves (both right and left) were measured separately and no attempt was made to match up single valves. With complete shells, beak length was measured from the outside of the shell from the umbone to the anterior margin, rather than from inside, the method used for single valves. Inflation for complete specimens was measured across both valves then recorded as half that measurement for each valve.

Statistical analyses (discriminant function analysis and ANOVA) of the measurements were conducted using SYSTAT, version 7.0.1 (SPSS, Chicago, IL, USA).

Wet material of each species was examined, and comparative preserved material of *Velesunio angasi* (Sowerby, 1867) (AMS C.420524) and *Alathyria jacksoni* Iredale, 1934 (AMS C.420521) was also examined. Except where noted otherwise, material examined is held in the Australian Museum, Sydney (AMS).

Abbreviations used in material examined

Institutions:
AMS   Australian Museum, Sydney
NTM   Northern Territory Museum and Art Gallery, Darwin
WAM   Western Australian Museum, Perth

Other abbreviations:
Hwy   Highway
HS   Homestead
nr   near
pr   pair (of valves)
R   River
Rd   Road
v   valve(s) (of shell)

Locality records

Material examined from the AMS and WAM is listed under 'Material examined' for each species. Two records from the NTM have not been checked by the authors and are listed under 'Additional records'.

Results

A summary of the samples measured is given in Table 1. These data were analysed to test the hypothesis that three species-group taxa could be recognised morphometrically. The third species is described below as *L. opertanea* n. sp. A discriminant function analysis accurately separated 88% of all three species using the measurement data ($P < 0.0001$): 88% of *L. froggatti* (20 out of 177 were misclassified as *L. opertanea* n. sp. and one as *L. rugata*), 83% of *L. rugata* (12 out of 70 misidentified as *L. opertanea* n. sp.) and 94% of *L. opertanea* n. sp. (three out of 100 misclassified as *L. rugata* and three as *L. froggatti*). A further analysis was carried out to test the distinctiveness of Western Australian (vicinity of Kalumburu, Kimberley) specimens, which are morphologically similar to the Northern Territory specimens attributed to *L. opertanea* yet markedly disjunct. The results are presented in Table 2 and in Fig. 1 (see also 'Remarks' under *L. opertanea* n. sp.) The disjunct Western Australian and Northern Territory samples attributed here to *L. opertanea* are not considered to be sufficiently distinct for formal recognition using morphological data alone and, accordingly, only three taxa are recognised formally below.

Table 1. Summary of the samples measured
See 'Material examined' under each taxon for further details about each lot. The numbers following the registration numbers are the numbers of measured valves.

Species	Material
Lortiella rugata	Ord River, WA (C427600, 10; C427109, 6; C424069, 19; WAM S13756, 10); Victoria River, NT (C371676, 13; C313605, 3; C113749, 12; C424068, 4).
Lortiella froggatti	Lennard River, WA (holotype and paratypes, 31; WAM S13760, 2; WAM S13762, 3; WAM S13764, 3; WAM S13761, 13); Fitzroy River, WA (C202368, 88; C371699, 20; C414981, 12; C367894, 10).
Lortiella opertanea n. sp.	Katherine River, NT (holotype and paratypes, 6; C155936, 8; C113750, 6; C126339, 37); Douglas River, NT (C314474, 11); Daly River, NT (C386619, 2); King Edward River, WA (WAM S13755, 2; WAM S13772, 16; WAM S13753, 14).

NT, Northern Territory; WA, Western Australia.

Table 2. Classification matrix resulting from a discriminant function analysis in which the Western Australian specimens of *Lortiella opertanea* n. sp. have been separated from the 'typical' eastern (NT) samples of that species
The material originally classified as each species is distributed along the rows.

	L. frogatti	*L. rugata*	*L. opertanea* NT	*L. opertanea* WA	Correct (%)
L. frogatti	151	0	21	5	85
L. opertanea NT	1	1	53	13	78
L. opertanea WA	1	0	7	24	75
L. rugata	0	57	7	6	81
Total	153	58	88	48	82

Table 3 summarises the measurements and ratios for each species, with the Northern Territory and Western Australian material of *L. opertanea* separated. ANOVA analyses were carried out on all measurements and followed with a Bonferroni adjusted *post hoc* test. The results, with *L. opertanea* separated graphically, are summarised in Tables 3 and 4.

Taxonomy

Subfamily **VELESUNIONINAE** Iredale, 1934

Velesunioninae Iredale, 1934: 58 (as Velesunionae).
Lortiellinae Iredale, 1934: 58.

The gross anatomy of specimens of all three species of *Lortiella* was examined. They are all very similar to one another and characteristic of the Hyriidae in having a marsupium formed from the inner demibranch, an anterior attachment of the inner demibranchs near the labial palps and a small posterior perforation separating the supra and infrabranchial chambers. *Lortiella* also has all the important diagnostic anatomical features of Velesunioninae listed by McMichael and Hiscock (1958). These include: the smooth umbos; lamellar hinge; lack of a supraanal opening (this also seems to be a characteristic of the family); siphons not prominent or protruding; marsupium occupying at least two-thirds of the inner demibranch with the interlamellar junctions discontinuous; palps of medium to large size; glochidium subtriangular and hooked. The palps differ from those of

Table 3. Summary of measurement (mm) and ratio data: number of specimens measured, minimum to maximum (± standard deviation) and mean
The significance value (*P*), degrees of freedom (df) and *F*-ratio (*F*) were obtained from ANOVA. The Western Australian specimens of *Lortiella opertanea* n. sp. have been separated from the 'typical' eastern (NT) samples of that species.

Variable	L. rugata			L. froggatti			L. opertanea NT			L. opertanea WA			df	F	P
	n	Min–max ± SD	Mean	n	Min–max ± SD	Mean	n	Min–max ± SD	Mean	n	Min–max ± SD	Mean			
TL	74	22.55–116.05 ± 20.96	64.43	180	29.90–94.87 ± 10.66	58.00	70	35.35–71.65 ± 7.91	58.41	32	41.45–95.10 ± 11.99	60.25	352	4.41	0.005
MH	78	9.05–38.40 ± 6.22	21.55	181	14.95–38.70 ± 5.01	26.28	70	14.30–31.15 ± 3.15	23.21	32	18.00–40.35 ± 4.94	23.67	357	18.53	<0.001
BH	78	7.35–27.70 ± 4.74	16.99	182	13.35–34.80 ± 4.15	23.47	70	12.50 – 23.20 ± 2.25	19.21	32	12.90–31.05 ± 4.06	17.96	358	60.03	<0.001
W	74	2.53–13.40 ± 2.48	7.64	182	5.10–13.55 ± 1.66	9.13	68	4.70–11.45 ± 1.31	7.61	32	6.41–13.05 ± 1.53	8.35	352	18.50	<0.001
BL	76	6.25–29.50 ± 5.20	18.46	182	11.40–29.40 ± 3.61	19.99	70	10.90–22.60 ± 2.12	17.72	32	11.50–31.45 ± 4.33	17.22	356	9.35	<0.001
MH/TL	74	0.29–0.41 ± 0.02	0.34	178	0.35–0.55 ± 0.04	0.45	70	0.36–0.44 ± 0.02	0.40	32	0.36–0.49 ± 0.04	0.40	350	240.89	<0.001
BH/MH	78	0.60–0.90 ± 0.05	0.79	180	0.77–1.03 ± 0.05	0.90	70	0.73–1.03 ± 0.05	0.83	32	0.64–0.86 ± 0.05	0.76	356	131.68	<0.001
W/TL	70	0.10–0.15 ± 0.01	0.12	179	0.11–0.19 ± 0.01	0.16	70	0.09–0.16 ± 0.01	0.13	32	0.12–0.21 ± .02	0.14	345	204.03	<0.001
BH/TL	74	0.24–0.35 ± 0.03	0.29	179	0.27–0.41 ± 0.02	0.35	70	0.25 0.36 ± 0.03	0.31	32	0.22–0.44 ± 0.04	0.29	351	103.36	<0.001
BL/TL	74	0.22–0.33 ± 0.02	0.27	179	0.30–0.48 ± 0.04	0.41	70	0.29–0.38 ± 0.02	0.33	32	0.24–0.44 ± 0.04	0.30	351	379.95	<0.001

BH, height at beak measured from beak to ventral margin at 180° from beak; BL, length of beak measured from umbo to anterior end of shell along dorsal margin; MH, maximum height measured from dorsal margin to ventral margin; TL, total length as measured from anterior margin to posterior margin; W, width of a single valve.
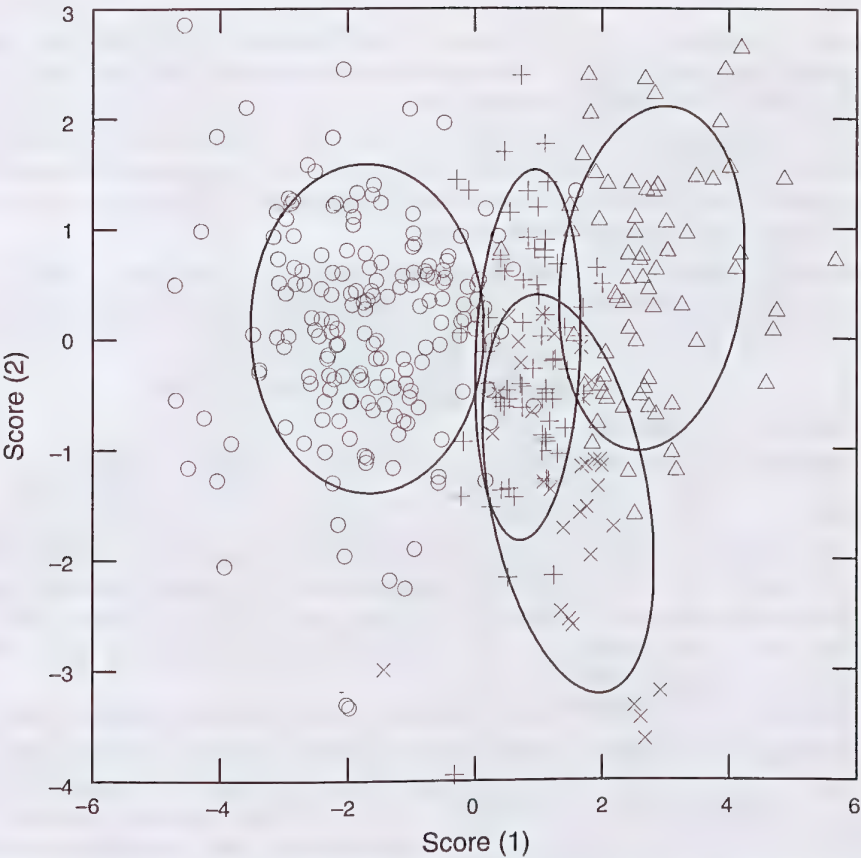
Fig. 1. Plot of discriminant function scores obtained from the non-ratio measurement data for all three species. △, *Lortiella rugata*; ○, *Lortiella froggatti*; +, Northern Territory populations of *Lortiella opertanea*; ×, Western Australian populations of *Lortiella opertanea*. The ellipses show signficance of *P* = 0.7.

Table 4. Summary of measurements and ratios of *Lortiella* taxa that are significantly different (*P* < 0.001 or *P* = 0.001–0.005, the latter in parentheses) using a Bonferroni adjusted *post hoc* test
The Western Australian specimens of *L. opertanea* n. sp. have been separated from the 'typical' eastern (NT) samples of that species.

	L. rugata	*L. froggatti*	*L. opertanea* NT
L. froggatti	(TL), BH, W, MH/TL, BH/MH, W/TL, BH/TL, BL/TL		
L. opertanea NT	MH, (BH), MH/TL, BH/MH, W/TL, BL/TL	MH, BH, W, BL, MH/TL, BH/MH, W/TL, BH/TL, BL/TL	
L. opertanea WA	(BH), MH/TL, (BH/MH), W/TL, BL/TL	BH, (BL), MH/TL, BH/MH, W/TL, BH/TL, BL/TL	BH/MH, BL/TL

Abbreviations as in Table 3.

Alathyria and *Velesunio* in being more truncated posteriorly, giving them an elongated triangular appearance. In contrast, *Alathyria* and *Velesunio* have 'semilunar' palps. McMichael and Hiscock (1958: 387) stated that the palps of *Velesunio* are triangular to subtriangular, but in their description of *V. wilsonii* (Lea) they state that the palps of that species are 'subtriangular to semilunar' (p.400). Given that there are no significant differences between Velesunioninae and Lortiellinae, we treat these taxa as synonyms. Because both family-group names were erected by Iredale (1934) on the same page we, as first revisers, give Velesunioninae precedence.

The nomenclatural details of the generic and specific taxa included in *Lortiella* were given in detail by McMichael and Hiscock (1958) and most of these data are not repeated here.

Genus *Lortiella* Iredale, 1934

Genus *Lortiella* Iredale, 1934: 70.
Type species: *Mycetopus rugatus* Sowerby, 1868.

Remarks

The type designation was cited as 'original designation' by McMichael and Hiscock (1958: 432) but Iredale (1934: 70) did not clearly designate *Mycetopus rugatus* as the type species and introduced *L. froggatti* as a new species on the next page. Similarly, Iredale (1943) did not designate a type species. The first subsequent designation appears to be that of McMichael and Hiscock (1958: 432).

McMichael and Hiscock's (1958) description of the genus included only the shell morphology and distribution. They described *Lortiella* as being up to 100 mm in length and having a MHI of 35–40%. The shell was described as 'somewhat adze-shaped, tapering anteriorly, somewhat winged posteriorly'. They noted that the genus is restricted to north-western Australia and that it can be distinguished from other Australian genus-group taxa by its low MHI and lack of beak and shell sculpture.

Lortiella rugata (Sowerby, 1868)

(Figs 2, 3*A–I*)

Mycetopus rugatus Sowerby, 1868: pl. 3, sp. and fig. 7.
Solenaia rugata; Simpson, 1900: 657; Simpson, 1914: 462.
Hyridella (Lortiella) rugata Haas, 1969*a*: N461, fig. D51:3.
Lortiella rugata; Iredale, 1934: 70; McMichael & Hiscock, 1958: pl. 9, figs 1, 2 (lectotype – see also
     Hiscock, 1960: 124); Haas, 1969*b*: 499.

Material examined

Northern Territory: Victoria R, ca 1.5 km upstream from bridge on Victoria Hwy, 15°36.0'S, 131°7.0'E (AMS, C.113749, 7 pr); Victoria R crossing, 15°36.817'S, 131°7.783'E (AMS, C.313605, 2); Victoria R, on Victoria Hwy, 15°36.89'S, 131°7.82'E (AMS, C.427938, 2 pr); Victoria R at Dashwood Crossing, 16°20.02'S, 131°6.86'E, (AMS, C.424068, 2); Victoria R at Coolibah Stn Rd, 15°33.30'S, 130°57.75'E (AMS, C.371676, 13 v). **Western Australia**: Ivanhoe crossing, 15°41.22'S, 128°41.23'E, under rocks and ledges (AMS, C.424069, 10); Kununurra, irrigation area, main supply channel, 15°46'S, 128°44'E (WAM S13758, 2 v; WAM S13757, 2 v; WAM S13759, 5 v); Ord R, 150 m below Kununurra Diversion Dam, on W side of river, 15°47.480'S, 128°41.580'E, under rocks and amongst roots and mud (AMS, C.427600, 6 pr); Lake Kununurra at Kona Caravan Park, 15°47.622'S, 128°43.136'E, in tube-like burrows in mud bank (AMS, C.427109, 3); Behn R, East Kimberley, nr Argyle Downs HS, 16°31'S, 128°55'E (WAM S13773, 1v); Ord R system, ca 1.5 miles downstream from Old Lissadell HS, 16°41'S, 128°33'E (WAM S13756, 20+).

Fig. 2. Distribution of the three species of *Lortiella*: O, *L. rugata*; +, *L. froggatti*; *, *L. opertanea*. (Da, Darwin; K, Kununurra; Ka, Katherine.)

Additional record

Northern Territory: 500 m above river gorge, upper reaches of Wickham R (tributary of Victoria R), SW of Darwin, 16°51.02′S, 130°14.00′E (NTM P010988, 2 pr).

Range and habitat

Victoria and Ord Rivers (Fig. 2); often living under large flat rocks.

Owen Griffiths provided the following information based on his observations made in July 2003 at Kona Caravan Park on the edge of Lake Kununnura, Western Australia. *Lortiella* were very common and found, each in their own burrow, on a steep muddy embankment from 10 to at least 50 cm below the lake surface. Each was ~5 cm inside the burrow, which was very narrow and fully occupied by the mussel, suggesting that they were not occupying a yabby (freshwater crayfish) burrow. They could be located by extending a finger down the burrow and touching the mussel shell. They had to be dug out as they could not be pulled out using forceps because they had their foot extended and were gripping the burrow wall. Over 20 were found in a 4-m stretch of embankment. Only one was located outside a burrow and this was wedged deep between rocks and appeared to be shorter and more stocky than those in the mud burrows.

Remarks

This species was described from material collected in the Victoria River on the second voyage of the Beagle (Iredale 1934; McMichael and Hiscock 1958). McMichael and
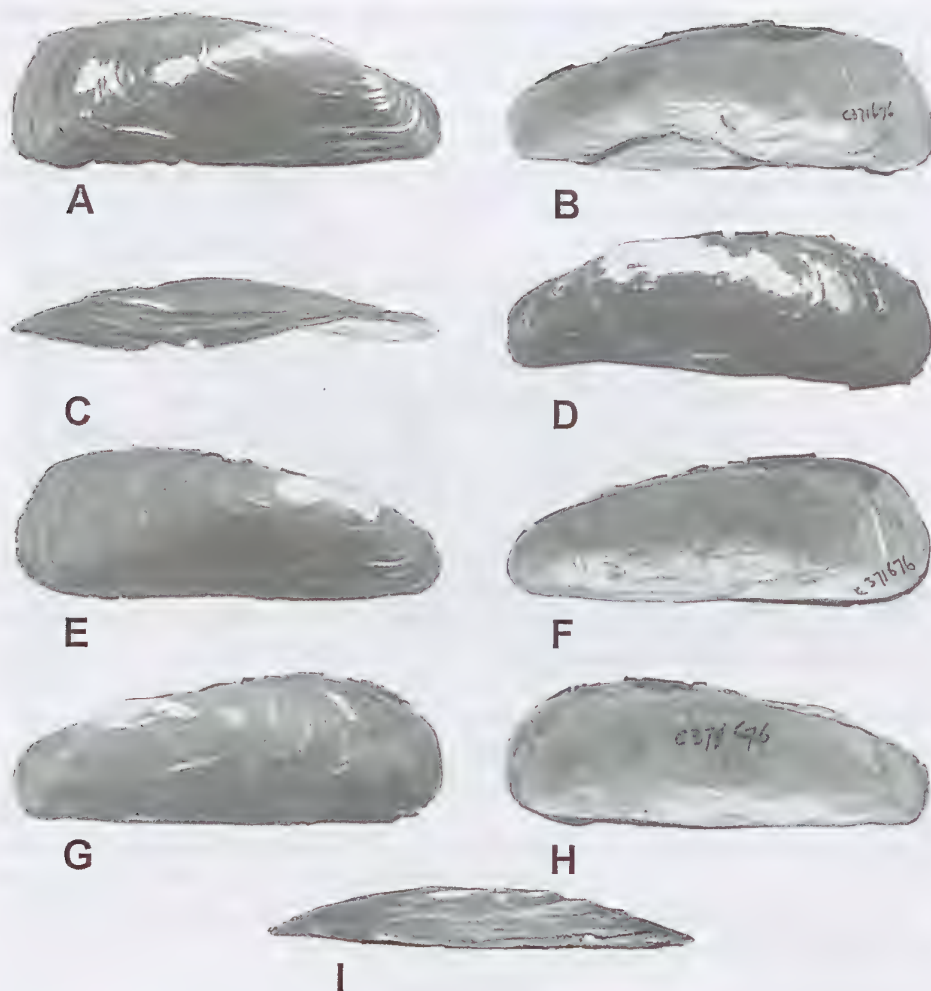
Fig. 3.   (*a–i*) *Lortiella rugata* (C.371676): (*a,d,e,g*) external view; (*b,f,h*) internal view; (*c,i*) ventral view. Shell lengths: (*a–c*) 90.70 mm; (*d*) 65.75 mm; (*g–i*) 55.90 mm.

Hiscock (1958) also recorded this species from the Katherine River and gave dimensions of two specimens from that locality. That material, however, is attributable to the new species described below.

Lortiella rugata is characterised by its very elongated, rather thin shell with a very reduced hinge and often squarely truncate posterior end (Fig. 3). The range of the MH/TL (i.e. MHI) is 29–41% (McMichael and Hiscock gave 35%), that of BH/MH (i.e. BHI) 60–91% (McMichael and Hiscock gave 75%) and the inflation *v.* length ratio is 10–15%. The ventral margin is straight to slightly concave, and sometimes distorted (e.g. Fig. 3*C*). The whole shell is slightly twisted in occasional specimens and this distortion, and that of the ventral margin, is presumably a consequence of the nestling (and/or burrowing) habit of this taxon. The periostracum is medium to dark brown and the internal nacre pearly white to silvery.
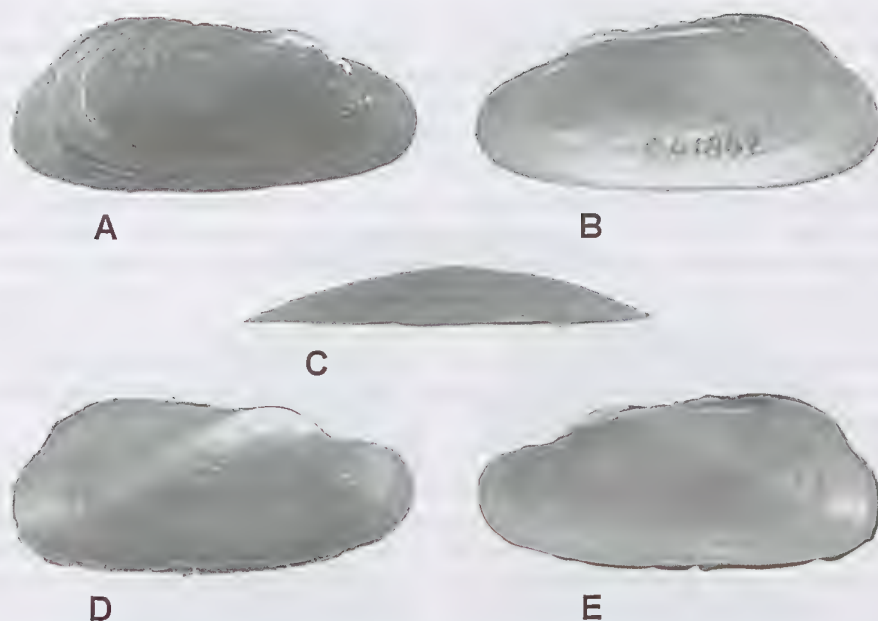
Fig. 4. (*a–e*) *Lortiella froggatti* ((*a–c*) C.61862, holotype; (*d,e*) C.427352): (*a,d*) external view; (*b,e*) internal view; (*c*) ventral view. Shell lengths: (*a–c*) 57.20 mm; (*d,e*) 51.90 mm.

Lortiella froggatti Iredale, 1934

(Figs 2, 4*A–E*)

Lortiella froggatti Iredale, 1934: 71, pl. 5, fig. 5 (holotype), pl. 6, fig. 5 (holotype); McMichael & Hiscock, 1958: 434, pl. 9, figs 3, 4 (holotype), 5 (paratype); Haas 1969*b*: 499.

Material examined

Holotype. Lennard R, Western Australia, 17°24.000′S, 124°30.000′E, in sand, 1887, W. W. Froggatt (AMS C.061862, 1 pr).

Paratypes. Same data as holotype (AMS C.061863, 29 v).

Other material: **Western Australia**: Fitzroy R, Sheepcamp Yard (WAM S13770, 4 v); Fitzroy R below Geike Gorge, 16°6.69′S, 125°41.85′E (C.371699, 20+); Charnley R, Walcott Inlet, 16°25.0′S, 124°57.0′E (C.126109, 1 v); Napier Ranges, NW end, 17°4′S, 124°39′E, (WAM S13765, 1 v); Lennard R, 17°24′S, 124°30′E (C.126279, 8 v); West Kimberley, Napier Ranges, Lennard R, Windjana Gorge, 17°25′S, 124°58′E (WAM S13762, 1 v); Napier Ranges, Windjana Gorge, 17°25′S, 124°58′E (WAM S13764, 9 v; WAM S13763, 11 v; WAM S13760, 4 v; WAM S13761, 20+); Fitzroy R, nr Willare Bridge nr Derby, 17°44′S, 123°39′E (WAM S13769, 1 v; WAM S13766, 2 v); Geike Gorge, Fitzroy R, 18°4′S, 125°44′E (C.414981, 7 pr; WAM S13768, 18 v; WAM S13771, 3 v); West Kimberley, Fitzroy R, Myroodah Crossing, 18°5′S, 124°13′E (WAM S1307, 8; WAM S13767, 1 v; WAM S13774, 6 v); Fitzroy R at Old Northern Hwy crossing, 18°10.75′S, 125°35.85′E (C.202368, 20+; C.367894, 5 pr; C.427352, 20+ pr).

Range and habit

Lennard River, Western Australia (types); Fitzroy and Charnley Rivers, western Kimberley, Western Australia (Fig. 2). Burrows shallowly in sand (W. Ponder pers. obs.).

Remarks

The shells of the type specimens of this species were described by Iredale (1934) and McMichael and Hiscock (1958). The shell of this taxon is obliquely truncate, rounded and

somewhat winged posteriorly, and is significantly more inflated than the other two species (Fig. 4; Tables 3, 4). The range of the MH/TL (MHI) is 40–55% (McMichael and Hiscock gave 40% based on only the type material). The range of the BH/MH (BHI) is 77–100% (McMichael and Hiscock gave 80%). The shell is typically thicker than that of *L. rugata* (and the new species described below). The posterior lateral hinge tooth is stronger in larger specimens than in the other two species and the ventral margin is moderately convex. McMichael and Hiscock described the periostracum as yellow-brown, marked by fine growth lines, the nacre as bluish iridescent and the shell substance thin. Although this accurately describes the juvenile type material, other lots of *L. froggatti* have a darker brown periostracum with fine growth lines (the growth lines are much more coarse in *L. rugata* and the new species). The nacre is bluish or silvery, with some yellow to yellow-orange coloration and the shell is moderately thick. The nacre in dead shells dulls quickly. The valves of this species are usually symmetrical, a few specimens being only very slightly twisted.

McMichael and Hiscock (1958) noted that *L. froggatti* looked different from *L. rugata*, but considered that because their locations are hundreds of miles apart, ecophenotypic differences were possible. Although they suggested the possibility that the two taxa could be conspecific, they accepted the separation of the species. Based on our observations, these two taxa are very distinct in shape, shell construction and periostracal development. They also have different habits, *L. froggatti* burrowing shallowly in sand rather than nestling beneath rocks or burrowing in mud banks. These differences may well imply a greater level of difference than assumed from their current congeneric status.

Lortiella opertanea n. sp

(Figs 2, 5*A*–*G*)

Material examined

Holotype. Katherine R, Northern Territory, below gorge, 14°19.23′S, 132°24.93′E, in pool alongside river, under stones, 10 June 2003, W. F. Ponder, J. C. Walker & L. Puslednik (AMS C.427618 with ethanol-preserved animal).

Paratypes. **Northern Territory**: Katherine R, below gorge, 14°19.23′S, 132°24.93′E, in pool alongside river, under stones, 10 June 2003, W. F. Ponder, J. C. Walker & L. Puslednik (AMS C.427619, 2 pr (shells broken), with ethanol-preserved animal); Katherine National Park, second gorge, 14°18′S, 132°25′E, in flood debris, April 1988, O. L. Griffiths (AMS C.155936, 7 v; NTM P26186, 2 v).

Other material. **Northern Territory**: Douglas R crossing, 13°40.09′S, 130°39.54′E (AMS C.314474, 7 pr); Oolloo Crossing, Daly R, 14°04.67′S, 131°15.00′E (AMS C.386619, 1); Katherine R, ca 20 km NW of Eva Valley Stn, 14°5.000′S, 132°43.500′E, under rocks in shallow water (AMS C.113750, 4 pr); Katherine R, 14°28′S, 132°16′E (AMS C.126339, 20+ v). **Western Australia**: Kalumburu Mission, 14°18′S, 126°38′E (WAM, 1315, 1 pr, 13755, 1 pr, 13772, 8 pr); nr Kalumburu Mission, Carson R (WAM, 13753, 5 pr); Kalumburu, on King Edward R, large pool, 14°18′S, 126°38′E (WAM, 13754, 2 pr).

Additional records

Northern Territory: Daly R, 1 km upstream of junction of Douglas R and Daly R, 13°50.43′S, 131°08.82′E (NTM P008576, 7 pr, 1 v).

Description

Shell thin (some empty shells rather delicate and brittle; Fig. 5); swollen at rounded posterior ridge, somewhat compressed anteriorly, slightly winged posteriorly. Beaks low and apparently without sculpture (eroded in all specimens). Shell elongate, BH/MH (MHI)
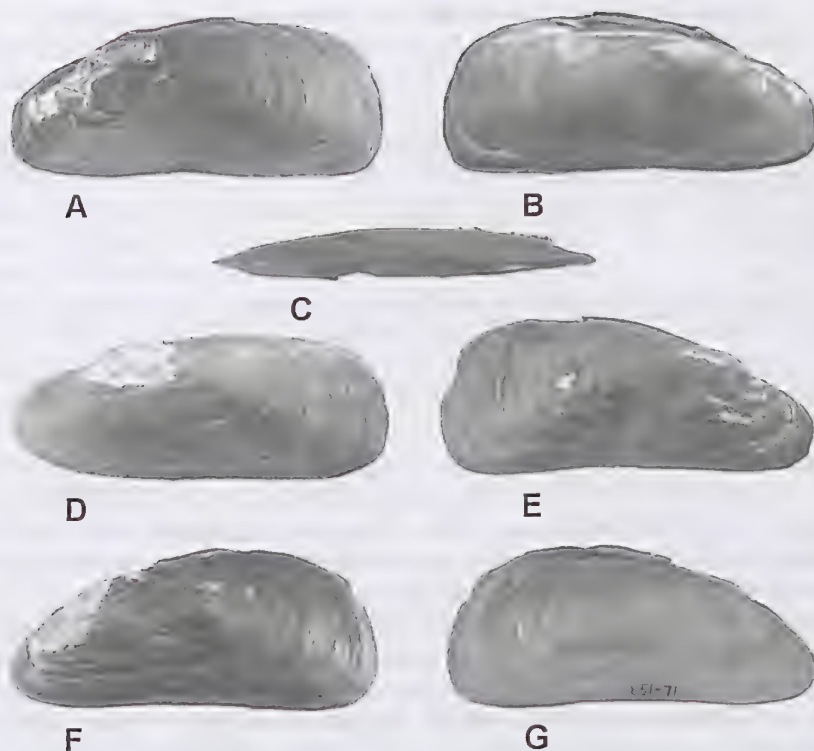
Fig. 5.   (*a–g*) *Lortiella opertanea* n. sp. ((*a–c*) C.427618, holotype; (*d,e*) C.126339; (*f,g*) WAM S13755): (*a,d–f*) external view; (*b,g*) internal view; (*c*) ventral view. Shell lengths: (*a–c*) 62.25 mm; (*d*) 52.40 mm; (*e*) 66.05 mm.

36–45%; anterior end relatively short (BL/TL 25–36%). Anterior margin truncate and rounded, ventral margin straight to slightly concave, rarely slightly convex; dorsal margin posterior to beak curved gently and elevated slightly (more so than in *L. rugata*), meeting posterior margin at rounded angle; BH/MH (BHI) 73–103%. Posterior margin truncate but usually rounded, rounded to subangled where it meets ventral margin. Interior nacreous, often pale bluish and/or with yellow tinge to dull golden brown. Hinge reduced, cardinal and anterior lateral teeth absent, posterior lateral tooth elongate, extending for about half posterior dorsal margin. Ligament well developed, external, extending about the same length as the posterior lateral tooth. Anterior and posterior muscle scars moderately impressed; retractor, protractor and adductor muscle scars fused. Pallial line moderately distinct. Periostracum well developed, dark brown, with prominent, often irregular and scaly commarginal growth lines. Dimensions are given in Tables 3 and 5.

Range and habit

Known only from the Katherine, Douglas and Daly Rivers, Northern Territory and the Carson/King Edward River System (vicinity of Kalumburu), Western Australia (Fig. 2). Found living beneath large flat rocks in pools in the riverbed where it generally lies on its side with the posterior end towards the outer edge of the stone.

Table 5. Dimensions of the type specimens of *Lortiella opertanea* n. sp. (mm)

	TL	MH	BH	W	BL
Holotype C427618					
Right valve	61.95	25.80	21.60	8.15	19.60
Left valve	62.10	25.70	21.40	7.60	20.85
Paratypes C427619					
Right valve	52.40	22.30	17.50	6.80	17.80
Left valve	52.25	22.50	17.55	6.80	17.10
Right valve	59.10	25.20	20.20	7.525	18.75
Left valve	58.90	25.25	20.50	7.525	18.75

Remarks

This species is not as narrowly elongate as *L. rugata* but is more elongate and compressed than *L. froggatti* (MH/TL and W/TL significantly different ($P < 0.001$) in all three species; Tables 3, 4). *Lortiella opertanea* is more similar to *L. rugata* but is not as flattened anteriorly. Like *L. rugata*, it is not as strongly calcified as *L. froggatti*, although it tends to be more calcified than *L. rugata*. The anterior end is not significantly different in length in *L. rugata* and *L. opertanea* but in both these species it is significantly shorter (measured as BL and relatively as BL/TL) than in *L. froggatti*. The posterior dorsal margin is usually distinctly convex in *L. opertanea* rather than flat or almost so in *L. rugata*. *L. opertanea* also has a higher posterior wing than *L. rugata* (measured as MH and relative to beak height as BH/MH and relative to total length as MH/TL, all of which differ at the $P < 0.001$ level; see also Tables 3, 4), but this wing is not as pronounced as in *L. froggatti*.

Specimens from the vicinity of Kalumburu (Kimberely, Western Australia) agree with the Northern Territory specimens in key shell characters and are assigned to *L. opertanea* on the basis of their similar shell morphology. However, 72% were discriminated successfully in a discriminant function analysis (Table 2; Fig. 1) and two ratios (BH/MH and BL/TL) were also significantly different at the $P < 0.001$ level. These differences are not considered, on their own, sufficiently great to recognise the specimens from the Kalumburu area as a distinct taxon. The markedly disjunct distribution of these populations from those in the Katherine, Douglas and Daly Rivers, with *Lortiella rugata* between them, may be explained by the new species having had a considerably wider distribution in the Pleistocene. It is, however, highly probable that two allopatric cryptic taxa will eventually be recognised when this taxonomy is tested with molecular data.

Discussion

Distinguishing species on shell morphology alone must always be treated with some caution, given the apparent ecophenotypic variation seen in some hyriid taxa (e.g. Walker 1981). Nevertheless, virtually all of the current species-level taxonomy of Australian freshwater mussels is based primarily on shell morphology with the exception of very recent work on some *Velesunio* taxa (Baker *et al.* 2003). McMichael and Hiscock's (1958) monograph placed the systematics of Australian Hyriidae on an excellent footing – and this is attested to by the fact that there have been very few changes to their conclusions in the 46 years since that revision. The recognition of an additional taxon in *Lortiella* using morphometrics was only possible after the acquisition of a large amount of new material

collected since that revision. However, despite the additional collecting that has occurred in tropical Australia, very few additional species of hyriids have been found that are separable morphologically.

Walker *et al.* (2001) discussed the status of Australian freshwater mussel systematics and noted the necessity for molecular studies to test the current taxonomy, a call repeated by Ponder and Walker (2003). The need for this was demonstrated recently by Baker *et al.* (2003), who provided molecular evidence that *Velesunio wilsonii* appears to be a polytypic species. Within the four lineages they identified, only one was distinctly separable morphologically, with the others showing considerable overlap.

The anatomical material available for this species, although not examined in great detail, has shown that *Lortiella* is not separable from Velesunioninae, as discussed above. However, these conclusions, together with the species-level taxonomy proposed herein, require further testing with molecular data. In particular, the markedly disjunct distribution of *L. opertanea*, as here recognised, needs to be further examined.

Acknowledgments

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A review of the genus *Enatimene* Iredale, 1929 (Gastropoda:Muricidae) from Australia

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Abstract

The three Australian species of *Enatimene* Iredale, 1929 are reviewed and illustrated: *E. simplex* (Hedley, 1903) from New South Wales, eastern Victoria and Tasmania; *E. bassetti* (Houart, 1998) from Queensland and New South Wales; and *E. lanceolatus* n. sp. from Queensland. *Enatimene* is compared with *Trophonopsis* Bucquoy & Dautzenberg, 1882.

Additional keywords: new species, taxonomy.

Introduction

The present paper deals with three Australian muricid species resembling the European *Trophonopsis* Bucquoy & Dautzenberg, 1882. Iredale (1929: 185–186) introduced several new generic and subgeneric names for muricids with little justification. *Enatimene* is considered to be Trophonine by recent authors (Radwin and D'Attilio 1976; Vaught 1989; Wilson 1994). However, since Trophoninae are now considered to be polyphyletic (Kool 1993*a*, Kool 1993*b*) (with the type species, *Trophon geversianus* (Pallas, 1774) proven more akin to *Nucella* Röding, 1798 (Ocenebrinae)), all these taxa, and many others, should be classified elsewhere—some possibly in Ocenebrinae. Their final placement, however, can only be determined after a careful study of all the taxa once considered as Trophoninae.

Enatimene Iredale, 1929 was described for *Trophon simplex* Hedley, 1903, a species closely resembling *Trophonopsis muricatus* (Montagu, 1803: fig. 15) from the Mediterranean Sea and the eastern Atlantic Ocean. A second species, *Enatimene bassetti* (Houart, 1998) was originally described in *Trophonopsis*. The discovery of a third species, described herein as new, has led to a thoughtful examination of the whole group and a careful comparison with *T. muricatus*. As a result, *Enatimene* is here retained as a valid taxon for the Australian species and separated from *Trophonopsis* on the basis of minor, although constant, differences.

Material and methods

All material examined is at AMS, and consists of dead shells, unless specified.

Terminology (after Merle 2001; Fig. 6)

The terminology used here is occasionally put between parentheses, meaning that the character was observed in a few cases but not in all specimens.

IP	Infrasutural primary cord (primary cord on shoulder)
P1	Shoulder primary cord
P2–P6	Primary cords of convex part of teleoconch whorl
s1–s6	Secondary cords
ADP	Adapical siphonal primary cord
MP	Median siphonal primary cord
ABP	Abapical siphonal primary cord

Aperture

ID	Infrasutural denticle
D1–D5	Denticles of the convex part of the teleoconch whorl
L	Length
W	Width
LA	Length of the aperture
LC	Length of the siphonal canal

Other abbreviations

AMS	Australian Museum, Sydney, Australia
HMAS	His/Her Majesty Australian Ship
MNHN	Muséum national d'Histoire naturelle, Paris, France

Systematics

Family **MURICIDAE** Rafinesque, 1815

Genus *Enatimene* Iredale, 1929

Enatimene Iredale, 1929: 185. Type species: *Trophon simplex* Hedley, 1903 (original designation).

Original description

'The little shell Hedley called *Trophon simplex* is a common member of the shelf fauna, and is generically named *Enatimene*, the small apex, medium spire, delicate shape, long recurved canal, and free mouth, making it a striking form, the sculpture being an obsolete clathration.' (Iredale, 1929: 185.)

Revised description

Shell fusiform with a high spire. Aperture ovate. Columellar lip smooth, rim partially erect, adherent adapically. Outer lip smooth or weakly undulate, occasionally with weak denticles within. Siphonal canal open, moderately long. Axial sculpture consisting of narrow ribs. Spiral sculpture of the convex part of teleoconch whorl consisting of narrow cords crossing the axial ribs.

Radula rachiglosse; rachidian with long, broad central cusp, short, narrow lateral denticles and broad, moderately long lateral cusps; lateral teeth sickle shaped, broad. Operculum pyriform with apical nucleus.

Remarks

The description of *Enatimene* is close to *Trophonopsis* Bucquoy & Dautzenberg, 1882, a taxon containing four European species (Houart 2001a): *T. muricatus* (Montagu, 1803) (type species); *T. barvicensis* (Johnston, 1825); *T. breviatus* (Jeffreys, 1882); and *T. droueti* (Dautzenberg, 1889). Other species classified in *Trophonopsis* by Egorov (1993) and by Houart (1994, 1998) have since been transferred to *Pagodula* Monterosato, 1884 (Houart 2001b) or to other genera, while others require further study to clarify their taxonomy. The three Australian *Enatimene* species have been compared with the type species of *Trophonopsis* and with each other. The shell of *Enatimene* resembles *T. muricatus* and the other European species, but differs in having a partially erect rim of the columellar lip in adult specimens (it is completely adherent in *Trophonopsis*), a mammillate protoconch (rounded and broad in *Trophonopsis*), and weak denticles within the outer apertural lip (strong and elongate in *Trophonopsis*).

Table 1.   Shell measurements (mm) of *Enatimene simplex*

Specimen	L	W	LA	LC
AMS C.322860	11.5	5.1	2.9	3.1
AMS C.322860	10.5	4.7	2.5	3.0
AMS C.322860	8.4	3.8	2.2	2.3
AMS C.322860	9.7	4.0	2.5	3.0
AMS C.322860	7.9	3.5	2.5	2.2
AMS C.322871	10.4	4.6	2.7	2.9
AMS C.322871	9.9	4.4	2.6	3.2
AMS C.322406	14.0	6.4	3.3	3.9
AMS C.322406	13.4	5.1	3.1	3.5
AMS C.322406	13.3	5.1	3.2	3.7
Mean	10.9	4.7	2.8	3.1

L, Length; LA, length of aperture; LC, length of siphonal canal; W, width.

Enatimene simplex (Hedley, 1903)

(Figs 1, 2, 4–14; Table 1)

Trophon simplex Hedley, 1903: 380, fig. 93
Enatimene simplex Iredale, 1929: 185. – May, 1958: 44, pl. 40, fig. 10; Radwin & D'Attilio, 1976: 180; Wilson, 1994: 51.

Material examined

Holotype.   Australia, New South Wales, off Port Kembla, 115–137 m (AMS C.16424).
Other material.   **New South Wales:** E of Coogee, Sydney, 33°56′S, 151°33′E, 146 m (1, C.322865); 28 km E of Little Bay, Sydney, 33°58.9′S, 151°33.63′E, alive, 183–192 m (13, C.322857); off Port Hacking, Sydney, 90 m (2, coll. R. Houart); off Botany Bay, Bay & Wattamolla, 34°4′S, 151°15′E, 91 m (8, C.322860); off Crookhaven, 34°55′S, 150°54′E, 64 m (23, C.322871); off Eden, 37°5′S, 150°10′E, 101 m (1, C.322859). **Tasmania:** off Cape Naturaliste, 40°50.6′S, 148°46.5′E, 399 m (11, C.322406); off St Helens Point, 41°20.6′S, 148°30′E, alive, 110 m (1, C.322402).

Other localities

New South Wales (Hedley 1903)**:** off Cape Three Points, 75–91 m; off Botany Bay, 91–95 m; off Wata Mooli, 99–108 m; of Crookhaven River, 20–27 m; off Port Hacking, 40–70 m; 26 km E of Wollongong, 183 m. **Eastern Victoria** (Wilson 1994: 51).

Description

Shell up to 14 mm in length at maturity (Table 1), creamy-white or light tan, lanceolate. Spire high, with 1.5–2 protoconch whorls, and up to 4–4.5 convex or weakly shouldered, teleoconch whorls. Suture impressed. Protoconch small, mammillate; whorls rounded, smooth; terminal varix low, straight.

Axial sculpture of teleoconch whorls consisting of low or moderately high, broad, occasionally weakly nodose ribs, occasionally obsolete on penultimate and last whorls. First teleoconch whorl with 11–13 ribs, second and third with 12–15, last whorl with 10–15 ribs. Apertural varix broadest and strongest. Other axial sculpture consisting of numerous growth striae. Spiral sculpture consisting of narrow, smooth or weakly nodose, primary and secondary cords. Last teleoconch whorl with IP, P1, P2, (s2), P3, s3, P4, (s4), P5, (s5), P6, ADP, (MP).

Aperture small, roundly ovate; columellar lip narrow, smooth; rim partially erect, adherent at adapical extremity; anal notch weak, broad; outer lip weakly erect, with five,
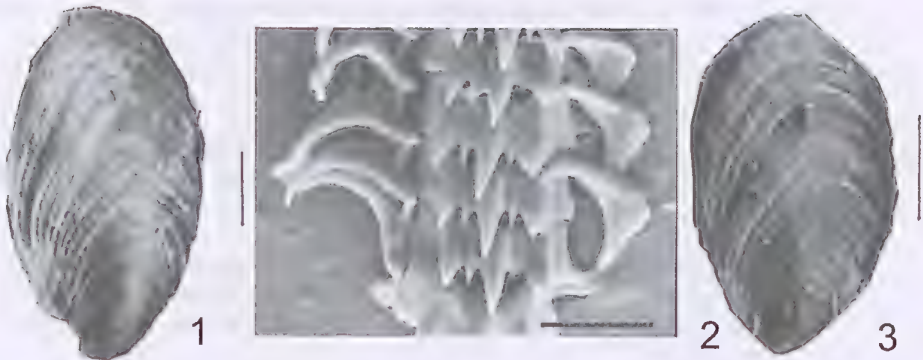
Figs 1–3.   *1*, Operculum of *Enatimene simplex* (scale bar: 0.5 mm); *2*, radula of *Enatimene simplex* (Hedley, 1903) (scale bar: 20 μm); *3*, operculum of *Enatimene lanceolatus* n. sp. (scale bar: 0.5 mm).
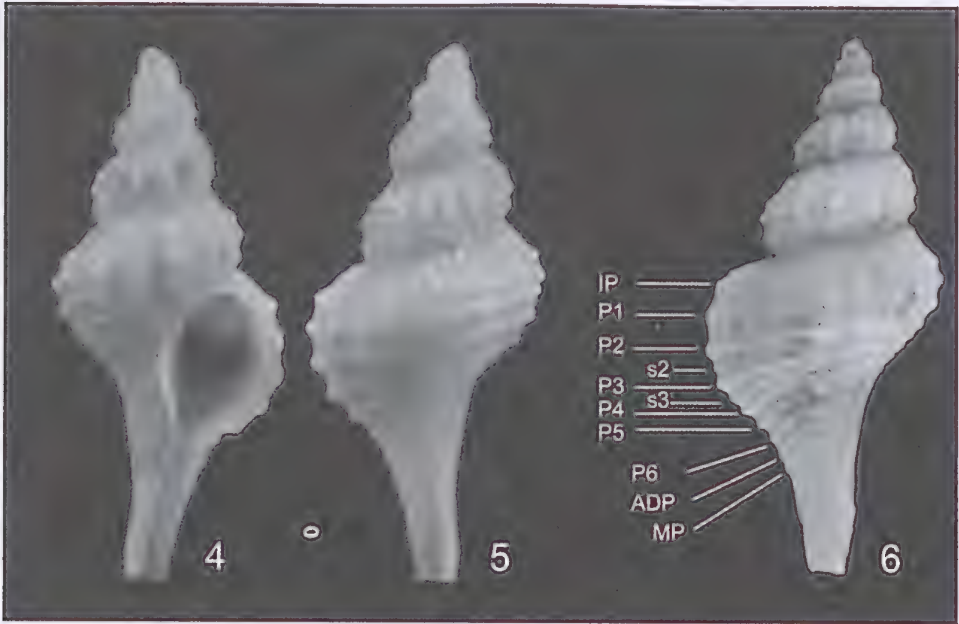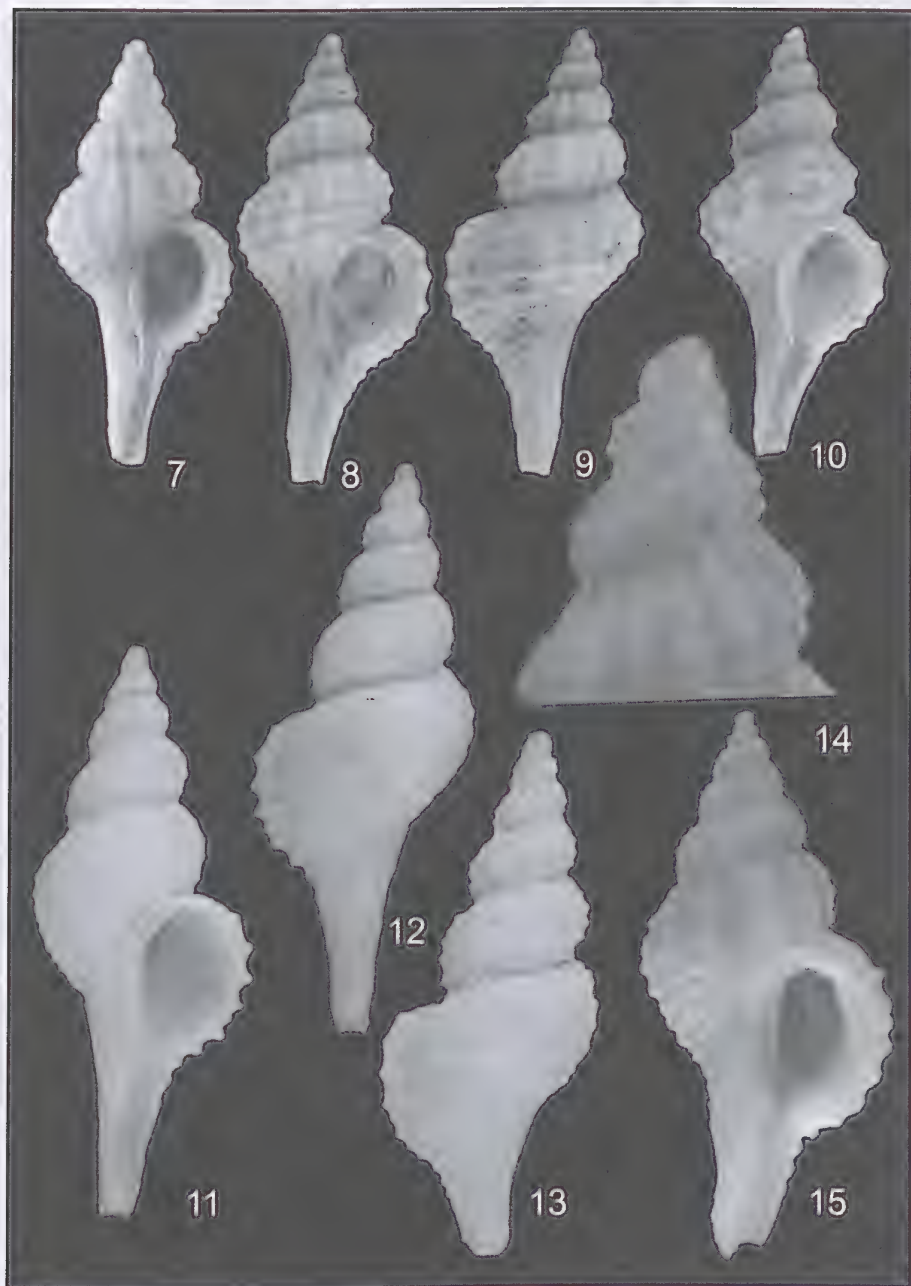

Figs 4–6.   *4–5, Enatimene simplex* (Hedley, 1903), holotype AMS C.16424, 8 mm; *6, E. simplex* AMS C.322860, New South Wales, (see also Figs 8–9), morphology of spiral sculpture (IP, infasutural primary cord; P1, shoulder primary cord; P2–P6, primary cords of convex part of teleoconch whorl; s2, s3, secondary cords; ADP, adapical siphonal primary cord; MP, median siphonal primary cord).

usually obsolete, weak denticles within. Siphonal canal long, straight, open. Operculum (Fig. 1) light brown, pyriform, with terminal nucleus.

Radula (Fig. 2): rachidian with long, broad central cusp, short, narrow, lateral denticle, and broad, irregularly shaped, lateral cusp. Lateral teeth sickle shaped, broad.

Distribution

Australia, from central New South Wales to Tasmania and eastern Victoria (33°56′S–41°20.6′S), 20–110 m.

Figs 7–15. *7–14, Enatimene simplex* (Hedley, 1903). *7*, New South Wales, Sydney, off Port Hacking, 1976, 11 mm, coll. R. Houart; *8–9*, AMS C.322860, New South Wales, off Botany Bay, Bay and Wattamolla, 34°4′S, 151°15′E, 91 m, 11.5 mm; *10*, AMS C.322871, New South Wales, off Crookhaven, 34°55′S, 150°54′E, 64 m, 10.4 mm; *11–13*, AMS C.322406, Tasmania, off Cape Naturaliste, 40°50.6′S, 148°46.5′E, 399 m; *11–12*, 14 mm; *13*, 13.7 mm; *14*, Holotype AMS C.16424, first teleoconch whorls. *15, Trophonopsis muricatus* (Montagu, 1803), AMS C.205289, Italy, Chioggia, 14 mm.

Remarks

The Tasmanian shells (Figs 11–13) are larger and slightly smoother than New South Wales specimens but otherwise no other differences could be detected. Their spiral sculpture, although shallower, is identical to that in the specimens from New South Wales. For differences with *E. bassetti* (Houart, 1998) and *E. lanceolatus* n. sp. see under these species.

Enatimene bassetti (Houart, 1998)

(Figs 16–18; Table 2)

Trophonopsis bassetti Houart, 1998: 100, figs 22–23, 47.

Material examined

Holotype. Australia, New South Wales, SE of Clarence River, 29°41′–29°32′S, 153°45–153°47′E, 405–412 m (AMS C.313223).
Paratypes. **Queensland**: E of Lady Musgrave Island, 23°52.5′–23°51.9′S, 152°42.7′–152°41.7′E, alive, 296 m (1, C.31323). **New South Wales**: SE of Clarence River, 29°41′–29°32′S, 153°45–153°47′E, 405–412 m (1, coll. R. Houart); E of Cape Three Points, 33°28′–33°29′S, 152°4′–152°3′E, 457–476 m (2, C.321596); off Sydney, 34°4.2′S, 151°37.4′E, alive, 393 m (1, C.322783); off Ulladulla, 35°30′–35°33′S, 150°48′–150°47′E, 549 m (1, C.313224).

Description

Shell medium-sized for the genus, up to 13.9 mm in length at maturity (Table 2), uniformly milky-white, slender, weakly spinose, delicate. Spire high, with 1.5 protoconch whorls and up to 4.5 shouldered, spinose teleoconch whorls. Suture impressed. Protoconch large, mammillate, glossy; terminal varix thin, low, weakly curved.

Axial sculpture of teleoconch whorls consisting of low, weak lamellae. Lamellae more strongly developed on shoulder, occasionally producing short, spinelike projections: 7 or 8 lamellae on first whorl, 10–12 on second, 11–13 on third, 11–15 on last whorl. Spiral sculpture consisting of broad, rounded cords: first, second and third whorl with two visible cords (P1 and P2), last whorl with IP, P1, P2, P3, P4, P5, P6, ADP.

Aperture moderately small, angulate; inner lip almost horizontal, forming an angle of ~85–86° with axis of shell; columellar lip smooth, adherent adapically, weakly erect abapically; anal notch shallow; outer lip smooth, with weak, low denticles within; adapical denticle more apparent. Siphonal canal medium-sized or long, narrow, straight, or weakly abaxially recurved, open.

Operculum and radula unknown.

Distribution

Australia, Queensland and New South Wales, 296–549 m, taken alive in 296–393 m.

Remarks

Enatimene simplex has a smoother, more convex shell with a roundly ovate aperture. The spire whorls are rounded or weakly shouldered (more strongly shouldered and spinose in *E. bassetti*), and secondary spiral cords are present (8–10 primary and secondary cords on last whorl, with a higher density on abapical part of the whorl), whereas secondary cords are absent in *E. bassetti*. For comparison with *Enatimene lanceolatus* n. sp. see under that species.
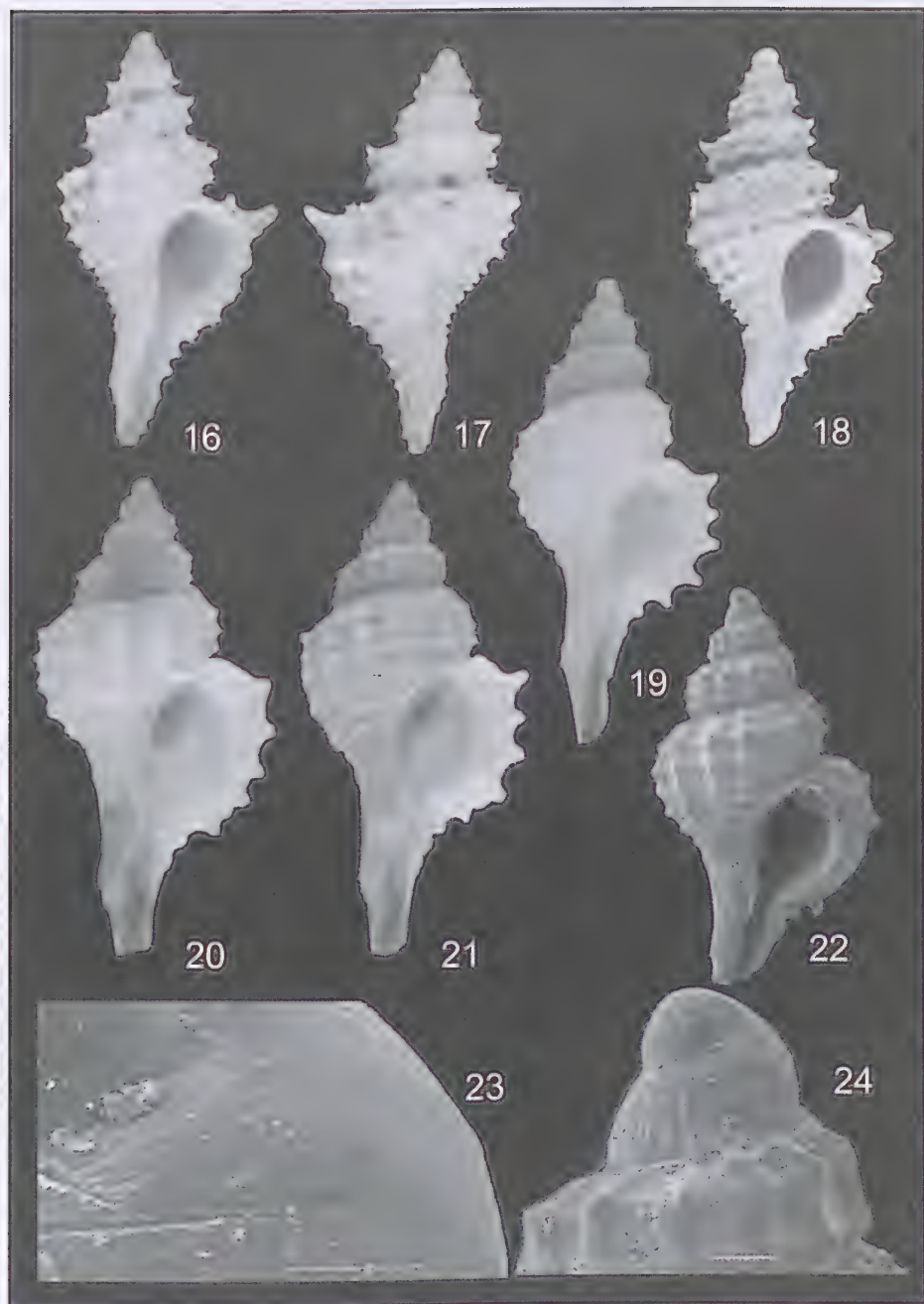
Figs 16–24.   *16–18, Enatimene bassetti* (Houart, 1998). *16–17*, Holotype, AMS C.3132238, 8.9 mm; *18*, Paratype, coll. R. Houart, 8.6 mm. *19–24,   Enatimene lanceolatus* n. sp. *19*, paratype AMS C.321986, 7.6 mm; *20*, holotype AMS C.427055, 8.5 mm; *21*, paratype AMS C.321986, 8 mm; *22–24*, paratype AMS C.321986, 6.6 mm (gold coated for s.e.m.) (scale bars: *23*: 100 μm; *24*: 200 μm).

Specimen	L	W	LA	LC
Holotype AMS C.313223	8.9	3.8	2.3	3.0
Paratype (R. Houart)	8.7	4.5	2.2	2.8
Mean	8.8	4.2	2.25	2.9

L, Length; LA, length of aperture; LC, length of siphonal canal; W, width.

Enatimene lanceolatus n. sp.

(Figs 3, 19–24; Table 3)

Material examined

Holotype.   Australia, Queensland, NE of Cape Moreton, 26°55.5′S, 153°33.5′E, alive, 115–124 m (AMS C.427055) (ex C.321986).

Paratypes.   **Queensland**: NE of Cape Moreton, 26°55.5′S, 153°33.5′E, alive, 115–124 m, pre 1968, T. A. Garrard coll. (6, C.321986, 1, MNHN); off Moreton Bay, 27°31′S, 153°40′E, 75–80 m (1, C.321918); off Cape Moreton, dredged alive in 104–121 m (1, coll. R. Houart).

Description

Shell small for the genus, up to 9.5 mm in length (paratypes AMS, Table 3), white or light tan, occasionally with brown band at abapical portion of siphonal canal; slender, lanceolate, nodose.

Spire high, with 1.5 protoconch whorls and up to four broadly convex, weakly shouldered, nodose teleoconch whorls. Suture impressed. Protoconch small, mamillate, with minute, scattered, raised granules (Figs 23, 24); terminal varix narrow, weakly raised and curved.

Axial sculpture of teleoconch whorls consisting of low or moderately high, broad, nodose ribs: 11 on first whorl, 12–14 on second, 12 or 13 on third, last whorl with eight axial ribs, and broad, strong apertural varix. Space between last axial rib of last teleoconch whorl and apertural varix twice (or more) as broad as space between other ribs. Spiral sculpture consisting of moderately high, narrow, nodose cords: first teleoconch whorl with visible P1, P2, (P3), second with visible P1, P2, P3, third whorl with P1–P6, ADP, fourth with P1, P2, P3, s3, P4, s4, P5, P6, ADP, (MP). Cords ending as short, broad, weakly acute, open spines on apertural varix. Spines of P1, P3–P5 almost similar in size, P2 smaller, P6 shortest.

Aperture large, broad, ovate. Columellar lip broad, smooth, rim partially erect, adherent at adapical extremity. Anal notch shallow, narrow. Outer lip erect, crenulate, with five weak denticles within (D1–D5). Siphonal canal, broad, straight, with one or two narrow spiral cords (ADP, occasionally MP). Operculum ovate with terminal nucleus (Fig. 3).

Radula unknown.

Remarks

Enatimene lanceolatus n. sp. differs from *E. simplex* (Figs 1, 2, 4–14) occurring off south-eastern Australia and Tasmania in having a smaller shell although the same number of teleoconch whorls, a broader, expanded apertural varix with short, broad, triangular, open spines (apertural spines absent in *E. simplex*), comparatively stouter and broader teleoconch whorls, and fewer secondary spiral cords; *E. simplex* usually having the following arrangement: IP, P1, P2, (s2), P3, s3, P4, (s4), P5, (s5), P6, ADP, (MP).

Table 3.   Shell measurements (mm) of *Enatimene lanceolatus* n. sp.

Specimen	L	W	LA	LC
Holotype AMS C. 427055	8.5	4.4	2.4	2.5
Paratype AMS C.321986	7.6	3.5	2.2	2.3
Paratype AMS C.321986	8.0	3.9	2.1	2.4
Paratype AMS C.321986	6.6	3.6	1.8	1.8
Paratype AMS C.321986	6.2	3.8	2.2	2.5
Paratype AMS C.321986	7.4	3.6	1.9	2.2
Paratype AMS C.321986	8.1	4.3	2.3	Broken
Paratype AMS C.321918	9.1	4.2	2.2	2.7
Paratype MNHN	7.7	3.8	2.1	2.5
Paratype R. Houart	8.8	4.3	2.1	2.9
Mean	7.8	3.9	2.1	2.4

L, Length, LA, length of aperture, LC, length of siphonal canal; W, width.

The new species differs from *E. bassetti* (Figs 16–18) from Queensland and New South Wales in having a more lanceolate and slender shell, compared to the more triangular outline of *E. bassetti*, fewer and more rounded axial ribs (eight on last whorl *v.* 11–15 in *T. bassetti*), and in the presence of secondary spiral cords, and comparatively narrower primary cords.

Etymology

Lanceolatus (Latin): spearlike.

Discussion

Enatimene is currently known to be endemic to south-eastern Australia, from Queensland (Lady Musgrave Island) to Tasmania (off St Helens Point). As noted above, *Enatimene* resembles *Trophonopsis* Bucquoy & Dautzenberg, 1882 but differs in a few, yet constant, morphological shell characters. However, this assumed separation needs to be tested with additional studies, other than shell characters, such as molecular analyses.

Enatimene is not the only muricid genus named by Iredale (1929), and assigned to Trophoninae by recent authors (Radwin and D'Attilio 1976; Vaught 1989; Wilson 1994; Houart 1995), that is currently considered to be endemic to Australia. Others (all named by Iredale 1929) are: *Anatrophon* (type species: *Trophon sarmentosus* Hedley & May, 1908, south-eastern Australia); *Benthoxystus* (type species: *Trophon columnarius* Hedley & May, 1908, south-eastern Australia), and *Xenotrophon* (type species: *Trophon euschema* Iredale, 1929, New South Wales). Other genera that were considered to be endemic to Australia until recently are: *Enixotrophon* Iredale, 1929 (type species: *Trophon carduelis* Watson, 1883), which is very close to *Pagodula* Monterosato, 1884, and could be a synonym. *Enatimene carduelis* was recently recorded from off the North Island and the west coast of the South Island, New Zealand (Marshall and Houart 1995). *Litozamia* Iredale, 1929 (type species: *Peristernia rudolphi* Brazier, 1894) was considered to be endemic to southern Australia until Houart (1995) described *Litozamia tropis* from north-eastern New Caledonia.

Species included in *Anatrophon*, *Benthoxystus*, and *Litozamia* differ from those in *Enatimene* in having a narrow shell with a very high spire, a short siphonal canal, and shouldered or strongly shouldered teleoconch whorls. *Xenotrophon euschema* is very

different in having a *Haustellum*-like shell with rounded, very broad, last teleoconch whorl, and a very long siphonal canal.

Apixystus Iredale, 1929 (type species: *Trophon stimuleus* Hedley, 1907) was synonymised with *Gemixystus* Iredale, 1929 (type species: *Trophon laminatus* Petterd, 1884) by Houart (2004) and occurs in the Chesterfield Reefs as well as in south-eastern Australia. *Gemixystus* differs from *Enatimene* in having a much smaller shell (7.2 mm as a maximum length in *Gemixystus*), and in having laminate, frilled axial lamellae instead of rounded, broad axial ribs like *Enatimene,* a broad, rounded aperture, and a very short siphonal canal.

Emozamia Iredale, 1929 (type species: *Murex licinus* Hedley & Petterd, 1906) is now known to belong to Coralliophilinae (Kosuge and Suzuki 1985; Wilson 1994), whereas *Ollaphon* Iredale, 1929 (type species: *Trophon molorthus* Hedley & May, 1908), a species originally included in Muricidae, is probably a fasciolariid.

Only two possible endemic Trophonine species, *Trophon segmentatus* Verco, 1908 from southern Australia, and *Trophon aberrans* Houart, 1991 from Queensland, do not fit in any of these genera. *Trophon segmentatus* was assigned to *Apixystus* (= *Gemixystus*) by Wilson (1994), but differs in being larger (shell up to 9.5 mm in length), with a higher spire, a more ovate aperture, a longer siphonal canal and broad, rounded spiral cords. *Trophon segmentatus* differs from the species here assigned to *Enatimene* in having a narrower shell with a shorter siphonal canal, a higher spire, weakly frilled, lamellose varices, a broad, rounded protoconch, and a broad, strongly erect, columellar lip. *Trophon aberrans* differs from *Enatimene* species in being smaller, in having a shorter siphonal canal, strongly shouldered teleoconch whorls, and more numerous axial ribs with short, adapical bent, acute, open spines at the intersection of the spiral cord P1.

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New Taxa

Two new species of *Murexsul* (Gastropoda : Muricidae) from Australia

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Abstract

Murexsul asper n. sp. is described from Western Australia and is compared with *M. auratus* Kuroda & Habe, 1971 from Japan; *M. queenslandicus* n. sp. is described from Queensland. Both new species lie in a group of small species, including *M. charcoti* (Houart, 1991) and *M. micra* (Houart, 2001), from New Caledonia.

Introduction

Few recent studies have been made on small Australian muricids and consequently this fauna is poorly known. This is highlighted by the Muricidae in the collection of the Australian Museum, Sydney, in which several little known or unknown species were found (Houart 1998; Houart 2004). Among these were two species belonging to a group of species previously studied by Merle and Houart (2003), many of which have been classified in *Muricopsis (Murexsul)* or in *Murexsul* s.s. by Houart (1988, 1991, 1993, 1994, 2001*a,b*).

No radula was available for *M. asper* n. sp. because the material was collected dead, but a comparison with related species for which the radula morphology is known, together with the peculiar shell morphology of the species, leave no doubt about its current classification in Muricopsinae.

Material and methods

All material examined is at AMS, and consists of dead shells, unless specified.

Terminology (following Merle 2001; Figs 11, 12)

The terminology used here is occasionally put between parentheses, meaning that the character was observed in a few cases but not in all specimens.

abis	Abapical infrasutural secondary cord (shoulder)
IP	Infrasutural primary cord (primary cord on shoulder)
P1	Shoulder primary cord
P2–P6	Primary cords of convex part of teleoconch whorl
s1–s6	Secondary cords
ADP	Adapical siphonal primary cord
L	Length
W	Width
LA	Length of the aperture
LC	Length of the siphonal canal

Other abbreviations

AMS	Australian Museum, Sydney, Australia
HMAS	His/Her Majesty Australian Ship
IRSNB	Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium

MNHN   Muséum national d'Histoire naturelle, Paris, France
QM   Queensland Museum, Brisbane, Australia
WAM   Western Australian Museum, Perth, Australia

Systematics

Family **MURICIDAE** Rafinesque, 1815

Subfamily **MURICOPSINAE** Radwin & d'Attilio, 1971

Genus *Murexsul* Iredale, 1915

Murexsul Iredale, 1915: 471. Type species: *Murex octogonus* Quoy & Gaimard, 1832 (original designation).

Murexsul asper n. sp.

(Figs 1–3, 13; Table 1)

Material examined

Holotype. Western Australia, Great Australian Bight, 33°20′S, 128°45′E, 140–147 m (AMS C.427056) (ex C.322392).

Paratypes. **Western Australia**: Great Australian Bight, 33°20′S, 128°45′E, 140–147 m, HMAS 'Gascoyne', 5 July 1962 (4, AMS C.322392); Great Australian Bight, 33°5–33°20′S, 128°40′–128°45′E, 75–147 m, HMAS 'Gascoyne', 5 July 1962 (3, AMS C.323254) (1, WAM S 13775, ex AMS C.323254); Great Australian Bight, 33°5′S, 128°45′E, 75–147 m, HMAS 'Gascoyne', 5 July 1962, (1, coll. R. Houart, ex AMS C.323252).

Description

Shell small for the genus, up to 8.6 mm in length at maturity (paratype C.322392, Table 1), white, lanceolate, weakly nodose.

Spire high with two protoconch whorls and up to five convex, elongate, weakly shouldered teleoconch whorls, suture impressed. Protoconch large, whorls rounded, smooth (Fig. 3), terminal varix heavy, raised, weakly curved.

Axial sculpture of teleoconch whorls consisting of erratically placed, low or moderately high, weak or strong ribs. Last whorl with five moderately high varices with weak intervarical ridges or lamellae. Intersection of axial ridges and spiral cords giving rise to small nodes. Spiral sculpture of high, strong, primary and secondary cords. First whorl with visible IP, P1 and P2, second whorl with IP, P1, P2, P3, third with IP, P1, P2, s2, P3, starting s1 at the end of the whorl, fourth whorl with IP, P1, s1, P2, s2, P3, fifth with IP, abis, P1, s1, P2, s2, P3, P4, P5 (probably), s5 (probably), P6, ADP.

Aperture large, roundly-ovate, columellar lip broad, smooth, rim partially erect, adherent at adapical extremity, anal notch not visible in studied specimens. Outer lip weakly erect, smooth within. Siphonal canal moderate in length for the genus, broad, straight, open.

Operculum and radula unknown.

Distribution

Western Australia, 33°20′S, 128°45′E, 75–147 m.

Remarks

One species, *Murexsul auratus* Kuroda & Habe, 1971 (Figs 15, 16), most closely resembles *M. asper*, but has a higher spire, a shorter siphonal canal, broader, more obvious spiral cords

Figs 1–10. *1–3, Murexsul asper* n. sp., Western Australia, Great Australian Bight, 33°20′S, 128°45′E, 140–147 m (uncoated s.e.m.): *1*, holotype (AMS C.427056, ex C.322392) 7.5 mm; *2–3*, paratype (AMS C.322392), 6.0 mm. *4–10, Murexsul queenslandicus* n. sp. Australia, Queensland, SE of Swain Reefs. 22°26.27′–22°20.2′S, 153°17.13′–152°17.6′E: *4–5*, holotype (AMS C.427057, ex C.321900) 4.3 mm; *6*, paratype (AMS C.321900), 4.3 mm (gold coated for s.e.m.); *7*, paratype (AMS C.321900), 4.5 mm (gold coated for s.e.m.); *8–10*, paratype (AMS C.321900) (gold coated for s.e.m.). *8*, protoconch; *9*, detail of the protoconch; *10*, detail of teleoconch spiral sculpture (scale bars: *3*, 500 μm; *8*, 200 μm; *9, 10*, 100 μm).

Table 1.   Shell measurements (mm) of *Murexsul asper* n. sp.

Specimen	L	W	LA	LC
Holotype AMS C.427056	7.5	3.9	2.1	1.7
Paratype AMS C.322392	6.0	3.0	1.6	1.5
Paratype AMS C.323254	6.5	3.1	1.9	1.3
Paratype AMS C.323254	7.3	3.6	2.0	1.6
Paratype AMS C.322392	8.6	Partially broken		
Paratype AMS C.322392	6.1	Partially broken		
Paratype WAM S13775	5.8	2.9	1.6	1.2
Paratype R. Houart	6.9	3.1	1.9	1.5
Mean	6.8	3.3	1.9	1.5

L, length; LA, length of the aperture; LC, length of the siphonal canal; W, width.

and more acute, short spines on the last whorl varices, and a more rounded, smaller aperture.

An unnamed species occurring off South Africa (coll. D. Meyer and Natal Museum) (Fig. 17) resembles the new species and could be the same, although more material is needed before a more definite comparison can be made.

Etymology

Asper (Latin): rough, uneven. For the uneven spiral sculpture.

Murexsul queenslandicus n. sp.

(Figs 4–12; Table 2)

Material examined

   Holotype.   Queensland, SE of Swain Reefs, 22°26.27′–22°20.2′S, 153°17.13′–152°17.6E, 187 m (AMS C.427057, ex C.321900).
   Paratypes. **Australia,   Queensland:**   SE   of   Swain   Reefs,   22°26.27′–22°20.2′S, 153°17.13′–152°17.6′E, 187 m, HMAS 'Kimbla', 5 July 1984, stn 7 (1, AMS C.321906); 22°26.27′–22°20.2′S, 153°17.13′–152°17.6′E, 187 m, HMAS 'Kimbla', 5 July 1984, stn 7 (79, AMS C.321900) (2 gold coated for s.e.m.), (2, QM MO 72376), (2, IRSNB IG 29980), (2, MNHN), (2, coll. R. Houart, all ex AMS C.321900); alive and dead; Capricorn Channel, 23°8.6′S, 152°16.6′E, 155 m, HMAS 'Kimbla', stn 21 (2, AMS C.321953).

Description

Shell small sized for the genus, up to 4.5 mm in length (Table 2), white, broadly biconical, spinose, nodose. Spire high with one protoconch whorl, and up to three broad, strongly angulate, spinose teleoconch whorls; suture impressed. Protoconch large, broad, whorl rounded, with rows of minute, raised granules on second part of protoconch (Figs 8, 9), terminal varix thin, weakly raised and curved.

   Axial sculpture of teleoconch whorls consisting of lamellae, ribs and varices: first whorl with seven or eight lamellae, second with four varices, third with three or four varices and three, or occasionally two, intervarical ribs. Spiral sculpture of high, strong, smooth, primary and secondary cords: visible part of first whorl with IP, P1, P2; second whorl with IP, P1, P2, P3, P4, (s4), P5, (P6); third whorl with IP, P1, s1, P2, (s2), P3, P4, s4, P5, P6. P1–P4 ending as short, blunt, open spines on varices, more apparent on apertural varix.
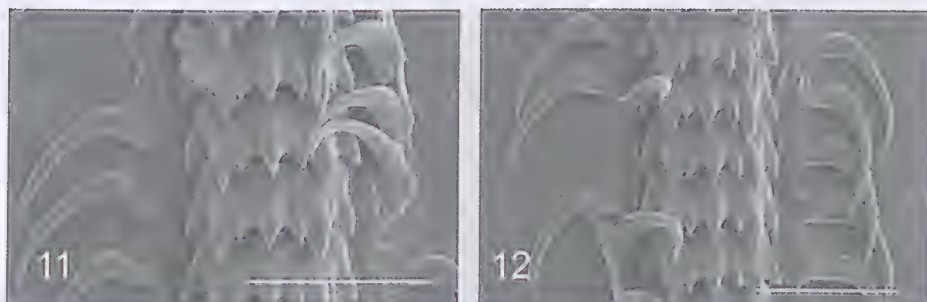
Figs 11–12. Radula of *Murexsul queenslandicus* n. sp. (scale bars: 12 μm).

Table 2.   Shell measurements (mm) of *Murexsul queenslandicus* n. sp.

Specimen	L	W	LA	LC
Holotype AMS C.427057	4.3	2.5	1.0	1.2
Paratype MNHN	4.0	2.7	1.0	0.9
Paratype MNHN	4.0	2.5	1.1	1.0
Paratype IRSNB IG 29980	4.0	2.3	1.0	1.1
Paratype IRSNB IG 29980	4.1	2.6	1.2	0.9
Paratype R. Houart	4.5	2.6	1.1	1.3
Paratype R. Houart	4.0	2.4	1.0	1.1
Paratype AMS C.321900	4.6	2.7	1.1	1.1
Paratype AMS C.321900	4.0	2.5	1.0	1.2
Paratype AMS C.321900	4.4	2.6	1.1	1.2
Mean	4.2	2.5	1.1	1.1

L, length; LA, length of the aperture; LC, length of the siphonal canal; W, width.

Aperture small, roundly ovate; columellar lip broad, flaring, smooth, rim partially erect, adherent at adapical extremity. Anal notch shallow, narrow. Outer lip weakly erect, smooth within. Siphonal canal moderately long, straight, narrowly open, smooth.

Radula (Figs 11, 12): rachidian with short, projecting median cusp, two short lateral denticles, two long lateral cusps with small outer lateral denticle, and two short marginal cusps; lateral teeth sickle-shaped, narrow.

Distribution

Australia, Queensland, SE of Swain Reefs and Capricorn Channel, in 155–187 m.

Remarks

Murexsul charcoti (Houart, 1991) (Figs 18, 19), from New Caledonia, is twice as long and broad for the same number of teleoconch whorls than *M. queenslandicus*; it also has a comparatively narrower apertural varix with broader and longer spines, lower and narrower axial ribs and different spiral sculpture consisting of P1, (s1), P2, P3, P4, P5 atrophied, P6 present or atrophied, on last teleoconch whorl. *Murexsul micra* (Houart, 2001; Figs 20–21), also from New Caledonia, differs from *M. charcoti* in its much smaller size and its different protoconch sculpture. It lives in much shallower depths, 20–35 m, compared with 394–450 m for *M. charcoti*. *Murexsul micra* differs from *M. queenslandicus* in having a
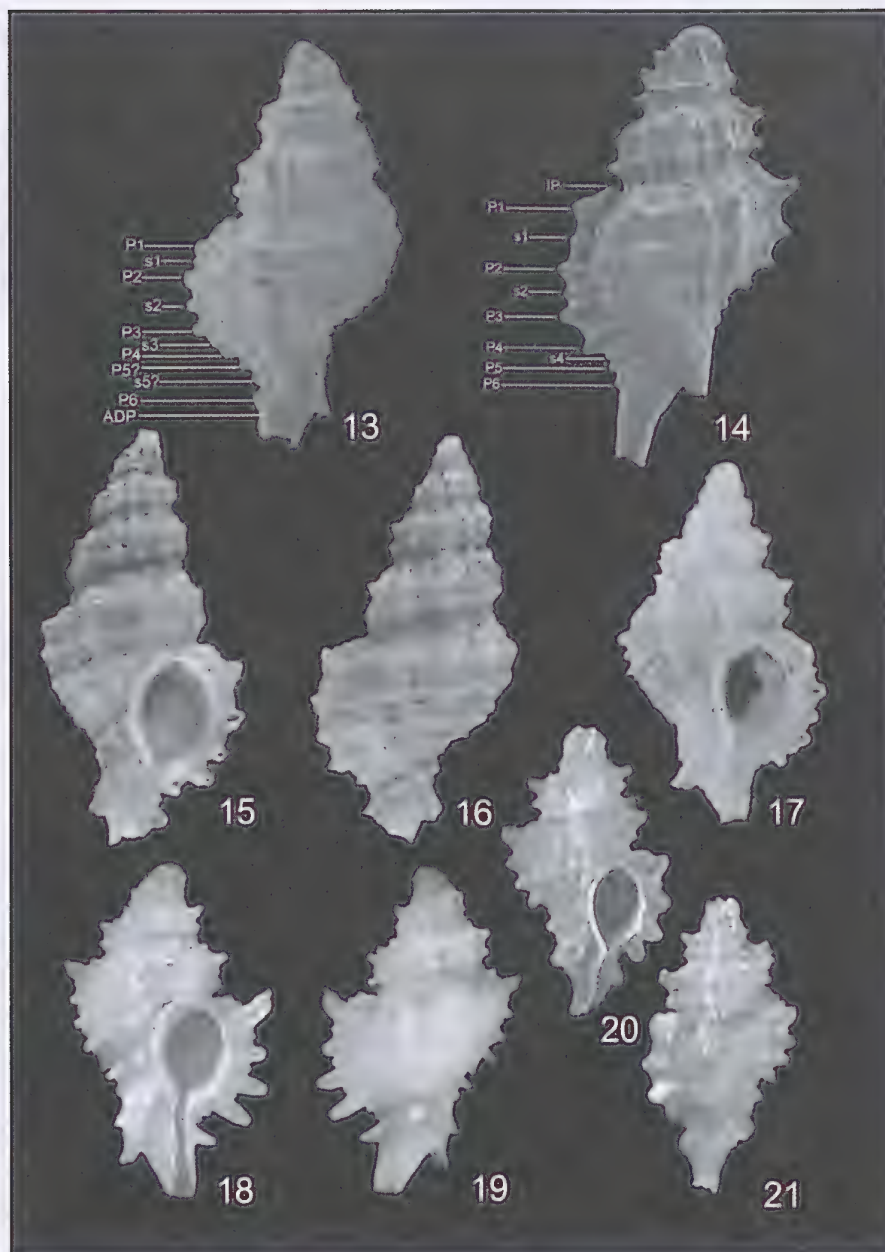
Figs 13–21. *13, Murexsul asper* n. sp., paratype (AMS C.322392), 5.8 mm, morphology of spiral sculpture; *14, Murexsul queenslandicus* n. sp., paratype (AMS C.321900), 4.5 mm, morphology of spiral sculpture (IP, infrasutural primary cord (primary cord on shoulder); P1, shoulder primary cord; P2–P6, primary cords of convex part of teleoconch whorl; s1–s5, secondary cords; ADP, adapical siphonal primary cord); *15–16, Murexsul auratus* Kuroda & Habe, 1971, holotype (NSMT-MOR 9605), Japan, Sagami Bay, 7.6 mm; *17, Murexsul* sp. Aliwal Shoal, 30–50 m, South Africa, 7.2 mm, coll. D. Meyer; *18–19, Murexsul charcoti* (Houart, 1991), holotype (MNHN), 7.2 mm, New Caledonia, 22°47′S, 167°14′E, 440–450 m; *20–21, Murexsul micra* (Houart, 2001), holotype (MNHN), 3.7 mm, New Caledonia, Grotte Merlet, 22°40.2′S, 166°37.9′E, 20–35 m.

narrower apertural varix with broader spines, a more ovate aperture with a narrower columellar lip, axial intervarical lamellae instead of ribs and spiral sculpture identical to *M. charcoti*.

These three taxa belong to a group of species distinguished from other *Murexsul* by their smaller shell with probable adults having less than five teleoconch whorls, and in having a broad, large protoconch of 1.0–1.5 whorls, indicating non-planktotrophic development.

Etymology

Queenslandicus: named after the Australian state, Queensland, where the type material was collected.

Discussion

Murexsul asper and *M. queenslandicus* both belong to a group of shells showing the assumed plesiomorphic condition of *Murexsul*, which comprises 19 Recent and fossil species from different parts of the world (Merle and Houart 2003). The plesiomorphic condition is assumed from the nature of the spiral sculpture (Merle and Houart 2003) determined from the condition in *M. prionotus* (Tate, 1888; Priabonian, Australia), which represents one of the oldest members of the genus (Merle 1999). The other Australian species included in that group are: *M. diamantina* (Houart, 1991), *M. planiliratus* (Reeve, 1845) and *M. purpurispina* (Ponder, 1972), but these species differ from the new species in shell length and other characters, especially in protoconch and spiral cord morphology.

Muricopsis asper has a reduced P5 spiral cord, a condition also seen in *Rolandiella* Marshall & Burch, 2000. However, *Rolandiella* differs also from *Murexsul*, in several characters not observed in *M. asper* and by the presence of a wider gap between the spirals P1 and P2.

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New Taxa

Two new *Fusinus* (Mollusca : Gastropoda : Fasciolariidae) from Western Australia

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Abstract

This paper describes two new *Fusinus* species in the neogastropod family Fasciolariidae: *Fusinus wellsi* n.
sp. and *Fusinus vercoi* n. sp., both from Western Australia. *Fusinus wellsi* n. sp. is similar to *Fusinus
leptorhynchus* (Tapparone-Canefri, 1875) from the Red Sea and *Fusinus vercoi* n. sp. is most similar to
Fusinus tessellatus (G. B. Sowerby, II, 1880), also from Western Australia.

Introduction

The fasciolariid genus *Fusinus* in the broad sense evolved in the Cretaceous period and
Recent species are spread worldwide through temperate waters. These gastropods have an
elongated shell with a tall spire and a long siphonal canal. Sculpture is typical of the family,
with axial ribs that are usually prominent, crossed by spiral cords. There are no columnellar
folds. Adults range in size from ~15 mm to more than 300 mm. The two new species
considered here are endemic to south-west Australia, joining *Fusinus tessellatus*
(G. B. Sowerby, II, 1880) and *Fusinus* (*Chryseofusus*) *westralis* Hadorn & Fraussen, 2003,
the only other *Fusinus* species endemic to this area. Other *Fusinus* collected from
south-west Australia range across southern Australia to New South Wales and often more
broadly into the Indo-Pacific region. All names assigned to this genus are enumerated in
Snyder (2003). These two species of *Fusinus* are typical of new fauna discovered in many
areas by diving and dredging. Commercial fishermen occasionally collect molluscs as part
of by-catch and salvage them for sale to collectors.

Methods

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell length is the maximum dimension
parallel to the axis of coiling. Shell width is measured perpendicular to the axis of coiling.

Institutional abbreviations

> ANSP   Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
> SC   Snyder Collection, Villanova, Pennsylvania, USA
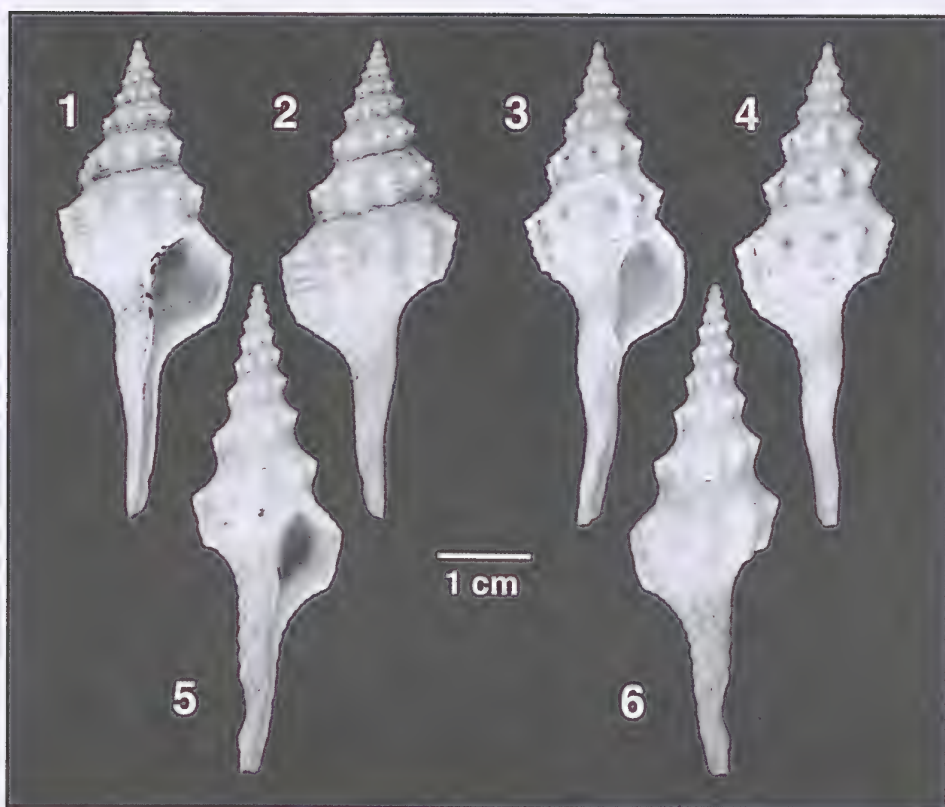> WAM   Western Australian Museum, Perth, Western Australia

Systematics

Family **FASCIOLARIIDAE** Gray, 1853

Subfamily **FUSININAE** Wrigley, 1927

Genus *Fusinus* Rafinesque, 1815

Type species: *Murex colus* Linnaeus, 1758, by monotypy. Recent, Indo-Pacific.

Figs 1–6.   *1, 2, Fusinus wellsi,* n. sp., holotype (WAM S14312). *3, 4, F. wellsi* n. sp., 59.1 mm, allegedly from fishing nets off Nha Trang, Vietnam (SC). *5, 6, F. leptorhynchus* (Tapparone-Canefri, 1875), 53.8 mm, collected off Shab Broor, Egypt (Red Sea) (SC).

Fusinus wellsi n. sp.

(Figs 1–4; Table 1)

Material examined

Holotype.   Western Australia, south-west of Dongara, 29°49′S 112°24′E, 128–132 m (WAM S14312).

Paratypes.   **Western Australia:** 1, 160 km north of Perth, off Cervantes, 20 m, in crayfish pots (WAM S13908); 1, off Albany, trawled at 100 m (SC); 1, south-west of Jurien Bay, 30°40′S 114°28′E, trawled at 139–146 m (WAM S10908); 1, west of Rottnest Island, 32°02′S 115°22′E, trawled at 109 m (WAM S10929).

Other material examined.   **Western Australia:** 2 (63.4 mm, 75.8 mm), 160 km north of Perth, off Cervantes, 20 m, in crayfish pots (SC). Twenty-nine lots of *Fusinus wellsi* n. sp. held in WAM were examined (specimen numbers greater than one in a lot are given prior to the locality; lots are grouped by locale, listed from north to south; F indicates a shell fragment): 2 + 2F, NW of Bluff Point, 27°40′S 113°03′E, 127 m, 1963 (WAM S10938); 2, W of Houtman Island, 28°52′S 113°53′E, 136–146 m, 1960 (WAM S10937); SW of Geralton, 29°05′S 113°56′E, 129–147 m, 1964 (WAM S10901); 29°07.5′S 113°57.5′E, 141 m, 1976 (WAM S10931); 1 + 2F, W of Dongara, 29°11.5′S 113°56.3′E, 137 m, 1976 (WAM S10904); 3, 29°15′S 114°01′E, 146 m, 1972 (WAM S10905); 19°14′S 114°04.5′E, 165 m, 1976 (WAM S10933); SW of Dongara, 29°28.2′S 114°11.1′E, 183 m, 1976 (WAM S10902); F, 29°33′S 114°19.5′E, 152–157 m, 1972 (WAM S10932); SW of Jurien Bay, 30°16.2′S 114°38.6′E, 137 m, 1976

(WAM S10906); 3, 30°40′S 114°28′E, 139–146 m, 1972 (WAM S10908); 30°21′S 114°38′E, 165 m, 1976 (WAM S10921); 2, 30°29′S 114°40′E, 145 m, 1970 (WAM S10930); 3, 30°38′S 114°47′E, 109 m, 1970 (WAM S10934); 13, W of Guilderton, 31°32′S 115°01′E, 146 m, 1972 (WAM S10910); NW of Rottnest Island, 32°00′S 115°30′E, 145–165 m, 1962 (WAM S10911); 32°00′S 115°30′E, 173–175 m, 1962 (WAM S10912); 32°00′S 115°30′E, 145–164 m, 1962 (WAM S10913); 2, 32°00′S 115°08′E, 136 m, 1963 (WAM S10914); 1 + 1F, 32°00′S 115°30′E, 145 m, 1965 (WAM S10915); 32°00′S 115°30′E, 182–187 m, 1962 (WAM S10916); 2, 32°00′S 115°30′E, 118 m, 1962 (WAM S10917); 32°00′S 115°30′E, 155–173 m, 1962 (WAM S10918); 32°00′S 115°30′E, 145–164 m, 1962 (WAM S10919); 4, 32°00′E 115°30′E, 145 m, 1965 (WAM S10920); 32°00′S 115°30′E, 176–182 m, 1965 (WAM S10922); 32°00′S 115°30′E, 135–144 m, 1962 (WAM S10923); 32°00′S 115°30′E, 127 m, 1965 (WAM S10924); 32°00′S 115°30′E, 164 m, 1965 (WAM S10925); 2, 32°00′S 115°30′E, 138–144 m, 1962 (WAM S10926); 32°00′S 115°30′E, 127 m, 1965 (WAM S10927); 4, 32°00′S 115°15′E, 146–150 m, 1972 (WAM S10928); 4 + 2F, 32°02′S 115°22′E, 109 m, 1970 (WAM S10929); 2 + 1F, NW of Bunbury, 33°00′S 114°37′E, 219–221 m, 1972 (WAM S10903); 2, NW of Cape Naturaliste, 33°40′S 114°28′E, 136 m, 1973 (WAM S10909). **Vietnam:** 1, 53.3 mm, off Nha Trang, from fishing nets (SC) (Figs 3, 4) [doubtful record].

Description

Shell length to 75.8 mm. Shell fusiform, moderate size for genus, moderately broad and heavy, with prominent axial and spiral sculpture. Protoconch with 1.75–2 smooth, bulbous, white glabrous whorls with narrow riblets on last half whorl. Transition to teleoconch abrupt, with coarser axial sculpture and onset of spiral sculptured whorls; teleoconch with 8–10 whorls. Axial sculpture dominant, consisting of 9–11 strong, angular ribs per whorl, aligned with spaces between ribs of previous whorl. Ribs angular on all whorls, forming sloping sutural ramp. Minute axial ridges and grooves between axial ribs. Spiral sculpture of strong cords; 2–4 on sutural ramp, one crossing axial ribs above ramp, forming nodules, 2–3 on abapical side of whorl; on body whorl four strong cords across raised central portion of axial rib with three weak cords between, ~10 strong cords along sloping concave neck and towards abapical end of canal. Aperture ovate, with well developed posterior canal. Columella thin, smooth, shiny white, adherent. Outer lip with rounded lirae, 1–2 mm wide. Inner lip shiny, white, with lirations 1.0–1.3 mm apart, terminating ~2.5 mm from periphery of lip. Siphonal canal long, straight to slightly sinuous. Shell colour white with randomly placed brown spots between axial ribs, usually centred on spiral cords. Operculum typically fasciolariid, caramel brown, claw-like, with terminal nucleus. Animal unknown.

Measurements

See Table 1.

Habitat and distribution

Occurs in moderately deep water from north-west of Bluff Point to north-west of Cape Naturaliste, a range of ~600 km.

Remarks

Fusinus wellsi, informally described and illustrated as *Fusinus* sp. by Wilson (1994: 69, pl. 13, fig. 6), has been collected in moderately deep water off Western Australia from 165 km west of Eucla (misidentified by Verco (1912: 221) as *Fusus novae-hollandiae*, at depth of 182 m) to Dongara. The twenty-nine WAM lots of *Fusinus wellsi* contain shells of lengths ranging from 24.8 mm to 56.9 mm. Four other WAM lots (WAM S10907, WAM S10935, WAM S10936, WAM S10939) contain immature specimens that can only questionably be assigned to this taxon. Lot WAM S10935 is probably *F. wellsi* and was supposedly collected west of Broome. This would represent a range extension of ~1250 km to the north. The

Table 1.   Shell dimensions of *Fusinus wellsi* n. sp. type material

	Length (mm)	Width (mm)	Length of aperture (mm)	Length of canal (mm)	Number of teleoconch whorls
Holotype					
WAM S14312	53.1	19.0	12	21	8
Paratypes					
WAM S13908	64.7	23.3	13	23	9
SC	59.1	19.3	12	22	9
WAM S10908	49.8	17.0	10	19	9
WAM S10929	44.7	15.8	8	17	8

species has allegedly been collected off Vietnam, but this may be a spurious record referring to a fishing vessel working from Vietnam.

Fusinus leptorhynchus (Tapparone-Canefri, 1875) (Figs 5, 6) is the species that appears to be most closely related to *F. wellsi*. This Red Sea species is somewhat larger (to 76.4 mm), has fewer axial ribs (8–9 on body whorl), and sometimes has random brown dots of colour, but often on the abapical side of the axial rib rather than by the sutural ramp. Larger Indo-Pacific *Fusinus* collected in Western Australia include *Fusinus* (*Chryseofusus*) *westralis* Hadorn & Fraussen, 2003, *F. colus* (Linnaeus, 1758), *F. nicobaricus* (Röding, 1798) and *F. undatus* (Gmelin, 1791). These are all well known species, figured in Wilson (1994) (*F. westralis* is illustrated as *Siphonofusus chrysodomoides*, pl. 12, fig. 7a, b) and quite different in form from *F. wellsi*. The smaller *F. tessellatus* (G. B. Sowerby, II, 1880), also from Western Australia, is discussed in detail below. This species has a stubby siphonal canal whereas *F. wellsi* has a long canal and a larger adult size. *Fusinus tessellatus* has rounded axial sculpture; the axial sculpture of *F. wellsi* is angular. Finally, *F. australis* (Quoy & Gaimard, 1833) is an endemic shallow-water species attaining a larger size; it is also well figured by Wilson (1994) and is a much broader, heavier species.

Etymology

This species is named for Dr Fred Wells of the Western Australian Museum who has done much to elucidate the Australian molluscan fauna.

Fusinus vercoi n. sp.

(Figs 7–10; Table 2)

Material examined

   Holotype.   Western Australia, off Albany, 30 m (WAM S13909).
   Paratypes.   **Western Australia:** 1, off Albany (type locality), 30 m (ANSP 410707); 1, off Fremantle, dredged at 25 m (SC); 1, Albany Harbour, 10–15 m, in weed and rubble (WAM S13910).
   Other material examined.   **Western Australia:** 4 (48.4–58.4 mm), Albany Harbour (SC).

Description

Shell length to 77.2 mm. Shell fusiform, moderate size for genus, broad and heavy, with prominent axial sculpture; spiral sculpture less prominent. Protoconch of two whorls, first 1 1/4 smooth, bulbous moderately depressed white with subsequent 3/4 whorl chocolate brown with fine axial line sculpture; early whorls slightly eroded and probably brown as well. Transition to teleoconch fairly well defined with coarser axial sculpture and onset of spiral sculptured whorls; 7–8 whorls in teleoconch. Axial sculpture dominant, consisting of
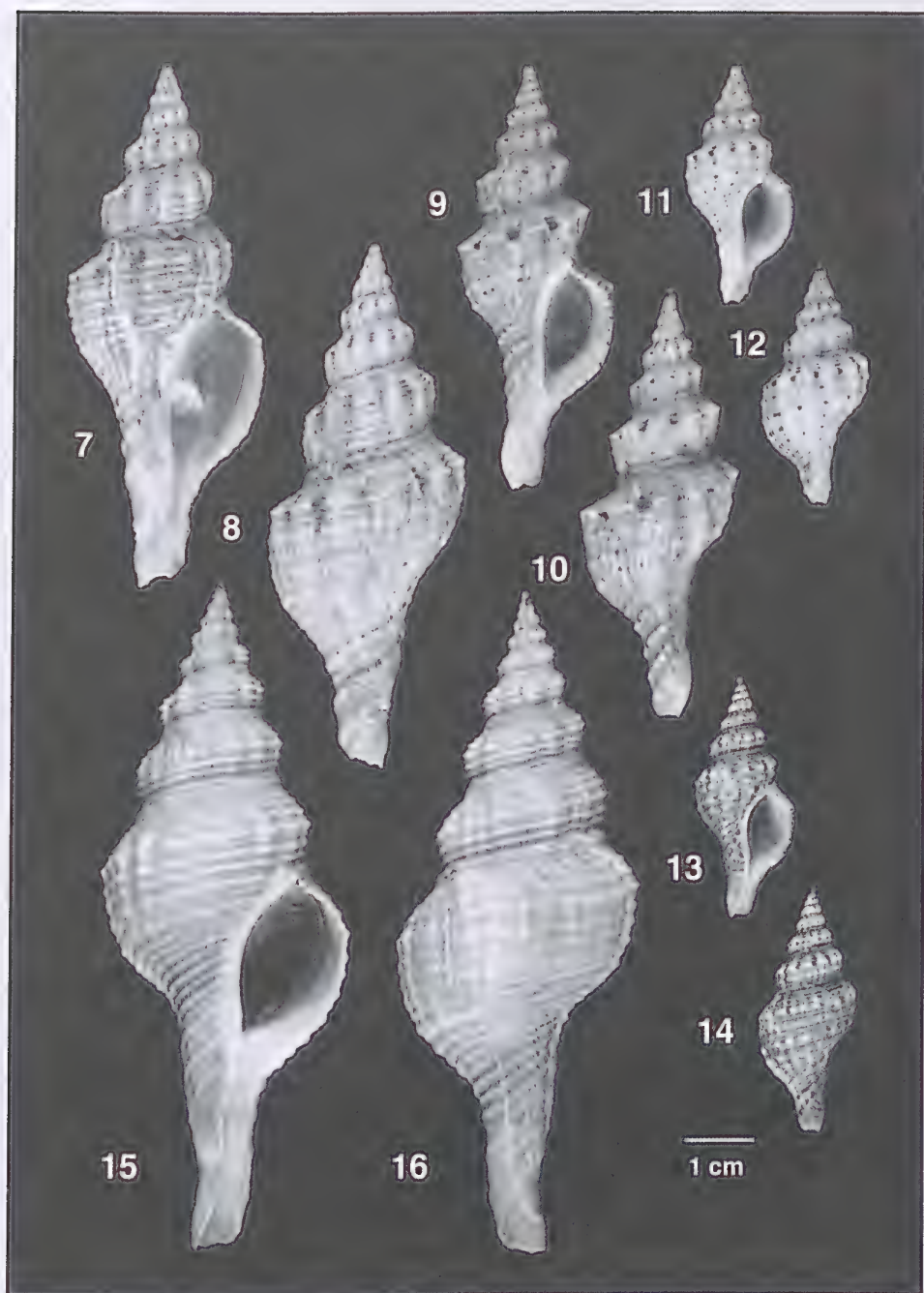
Figs 7–16.   *7, 8, Fusinus vercoi*, n. sp., holotype (WAM S13909). *9, 10, F. vercoi*, paratype (SC). *11, 12, F. tessellatus* (G. B. Sowerby, II, 1880), 37.2 mm, collected on reef in sand pockets, low tide, at Yallingup, Western Australia (SC). *13, 14, F. tessellatus*, 35.7 mm, collected with specimen in Figs 11, 12 (SC). *15, 16, F. australis* (Quoy & Gaimard, 1833), 96.6 mm, collected at 5–6 m, in sand, at Hyponga Beach, South Australia (SC).

Table 2.   Shell dimensions of *Fusinus vercoi* n. sp. type material

	Length (mm)	Width (mm)	Length of aperture (mm)	Length of canal (mm)	Number of teleoconch whorls
Holotype					
WAM S13909	77.2	30.2	25	18	8
Paratypes					
ANSP 410707	76.4	28.9	23	19	7
SC	63.4	23.9	19	16	8
WAM S13910	58.6	23.8	17	17	7

11–12 strong, angular ribs per whorl, aligned with spaces between ribs of previous whorl. Ribs angular on all whorls forming sloping sutural ramp; suture impressed. Fine axial ridges between and over axial ribs. Spiral sculpture of strong and weak cords; 2–5 weak cords between strong cords on sutural ramp, one crossing axial ribs above ramp, forming nodules; 3–4 on abapical side of whorl; on last whorl 9–10 strong cords to abapical end of canal. Aperture ovate, weakly developed anterior canal. Columella thin, smooth, shiny white, adherent in some specimens but often flaring at abapical end of aperture with prominent fold towards outer lip, constricting canal. Canal moderately long, slightly recurved away from plane of aperture, relatively closed. Outer lip with rounded dentations, ~1 mm wide, with brown colouration between dentations on most specimens. Inner lip shiny, white, with ~15–18 lirations stopping ~2.5 mm from periphery of lip. Shell colour mottled light-dark brown with white; dark brown spots often between axial nodules, towards sutural ramp, prominent on later whorls. Operculum typically fasciolariid, light to medium brown, clawlike, with terminal nucleus, filling aperture. Animal unknown.

Measurements

See Table 2.

Remarks

This species is closest to *Fusinus tessellatus* (G. B. Sowerby, II, 1880) (Figs 11–14), also from Western Australia, which, in addition to its smaller adult size, has a stubby, widely open siphonal canal. In most examples of *F. vercoi*, the columella is detached from the canal, folding towards the lip of the canal, restricting and almost closing the canal. On *F. tessellatus* the less prominent axial sculpture usually becomes obsolete on the last whorl. The prominent axial sculpture of *F. vercoi* remains pronounced on the last whorl, in many cases showing its strongest expression. The columellar shield is adherent in *F. tessellatus*, very rarely forming a slit-like sinus towards the abapical end of the canal. The protoconch of *F. tessellatus* is usually dark brown whereas the first embryonic whorls of *F. vercoi* are white. *F. tessellatus* is found intertidally among algae-covered rocks and collected from shallow reef tops. *Fusinus vercoi* is apparently confined to moderately deep water. Comparison may also be made with *F. australis* (Figs 15, 16). This variable species has a protoconch of nearly three whorls rather than two, has similar early-whorl sculpture, which becomes obsolete on the body whorl, and attains a much larger size, to 139 mm. *Fusinus australis* never has the dark brown spots between the axial knobs, as is usually the case in *F. vercoi*.

There is an additional taxon, which deserves consideration here: *Fusus philippii* Jonas, 1846. This species was briefly described, with no illustration, by Jonas (1846: 129) and

stated to be collected '*in litore occendentali Novae Hollandae*' (the western shore of Australia). The length and width of the shell is stated to be 15 lines (22.7 mm) and 6 lines (13.1 mm) respectively (for conversion factors see Abbott 1974: front flyleaf). The species is included by Philippi (1847: 191) and figured there (*Fusus* pl. 4, fig. 1). I believe that there is no extant type material of Jonas' taxon, and I have been unable to find any *Fusus* material of Philippi in either Germany or Chile. According to Dr Frank Koehler (Humboldt University, personal communication), the bulk of Jonas' material was held by the Hamburg Museum, which was completely destroyed in World War II. Conceivably one could use Philippi's figure for a lectotype designation of *Fusus philippii*, but the figure is not conclusively distinct. The figure more closely resembles *F. tessellatus* than *F. vercoi* and that observation coupled with the stated small size suggests that *F. philippii* may be the senior name of *F. tessellatus*. I think it is unlikely that this name could refer to the deeper-water *F. vercoi*. *Fusus philippii*, in any case, is probably best treated as a *nomen dubium* unless type material is subsequently discovered.

Etymology

This species is named for Sir Joseph Verco (1851–1933) who carried out numerous dredging expeditions along the southern and western coasts of Australia and first illustrated this species.

Discussion

The history and present view of the biogeography of Australia is discussed by Ponder and Wells (1998). The Australian marine species on the northern coast are part of the tropical Indo-West Pacific fauna, with low endemicity. *Fusinus vercoi* belongs to the southern Australian warmer temperate fauna (extending roughly as far west as Albany) where one finds many endemic species and it is likely endemic to that region. *Fusinus wellsi* belongs to the western overlap region where the southern temperate and northern tropical fauna meet. This widely distributed species is probably endemic to western Australia, although species occurring in the western overlap zone are reported to have lower endemicity than those found in the southern Australian temperate region. In each of these regions there is only one other endemic representative of the genus *Fusinus*, although the more widely distributed *F. australis* also occurs in the south-west.

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Obituary

Dr Paul Fischer, 1898–2003

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Obituary

Dr Paul Fischer, who died on 14 September 2003 at the age of 105, was a most remarkable and well-rounded man. Although foremost an eminent French zoologist, Paul was also a gracious and cultured family man, an accomplished musician and an enthusiastic historian.

Born on 14 February 1898, Paul became interested in science as a child. This is not surprising as both his parents came from scientific backgrounds with a particular interest in molluscs. His mother, Louise Piette, was the daughter of Edouard Piette (1827–1906), a renowned authority on prehistory and well known for his work on Jurassic gastropods. His grandfather, Paul Henri Fischer (1835–1893), took over the first international magazine on molluscs, the *Journal de Conchyliologie,* in 1856, from S. Petit de la Saussaye, who had founded this journal in 1850. This publication was continued by later generations of the Fischer family until 1979. His father, Henri Fischer (1865–1916), was a Doctor es Sciences, belonging to many European scientific associations. In Paul's own generation, his brother, Edouard Fischer-Piette (1899–1988) became a malacologist (Fischer-Piette 1968), while Paul himself was a generalist with wide-ranging interests in malacology. This tradition was to continue as Paul's son, Henri Jean Louis Fischer (1932–), in his turn, did some research on Antarctic molluscs. Also, Paul's daughter, Danielle, illustrated various articles of her father's in the *Journal de Conchyliologie* from 1969 onwards, as well as his 1959 book.

Paul had a happy childhood in a home frequented by scientists. Some of his father's friends were later to become famous, for example Louis Pasteur and Pierre and Marie Curie. His parents travelled often, taking him with them, and he acquired a taste for travel that never left him. In the year that he finished his schooling, 1916, his father died and his mother took over management of the *Journal de Conchyliologie*. This knowledgeable and capable woman directed and published the journal for nearly 40 years. It was under the auspices of the 'Journal' that, in 1935, a 'Malacological Re-union' took place in Paris (Anonymous 1935). This set the stage for the First European Malacological Congress in 1962, which grew into the World Congress as it is today. In contrast, Biggs (1965) claimed that the idea of an international malacological meeting originated at the 25th Anniversary of the Nederlandse Malacologische Vereniging in 1959, and downplayed Fischer's (1962) remark in a footnote: 'Dr P. H. Fischer … has mentioned that the idea of a European malacological organisation goes back at least to 1935.'

Paul started at the Sorbonne in 1917, but in April he was called up for military service in the First World War. He fought in the trenches until May the following year when he was wounded in action in Flanders. Subsequently he received the Military Cross and other decorations and was demobilised in 1919. Resuming his studies at university he became, in 1922, Licencie es-Sciences, and then Assistant in Zoology in the Sorbonne Faculty of Sciences.

Paul H. Fischer in 1928 and Paul wearing the newly awarded Legion d'Honneur, 1982.

During the early part of his career, Paul travelled frequently, in France, Greece, and Turkey, and undertook marine research in 1921 and 1925. He accompanied Jacques Cousteau on his first dives off the coast of Brittany at this time. Subsequently, he ventured even farther afield: in 1930 to Iceland and Norway (including Spitzbergen); in 1934 to Canada and the United States; and in 1938 to Australia. On all of these journeys he combined scientific research with enthusiastic observation of the countries, and still managed to take an active interest in the *Journal de Conchyliologie* – encouraging other scientists to publish in it, correcting proofs and undertaking some of the administrative work.

At the age of 37, Paul Fischer married Marie-Helene ('Lynette') Droulers. But this was not until after he had asked her to attend lectures at the Sorbonne on Zoology and Malacology. He thought she should have some idea of what her life would be like – shared with his other passion. A son, Henri Jean Louis, was born in 1936, and a daughter, Danielle Genevieve, in 1938. In 1939, aged 40, Paul was once more mobilised for military service. This time he fought in France but for health reasons was discharged in late 1940.

In 1944 he took up the position of Chef des Travaux Pratiques de Paleontologie at the Ecole des Mines de Paris. In 1949 he was appointed Dean of the University of Saigon. He was then Professeur Titulaire de Zoologie. After a scientific mission to Japan, he left Indo-China late in 1951, arriving back in Paris in 1952 where he resumed his functions at the Ecole des Mines as Conservateur de Collections Paleontologiques. In the following years he participated in many international zoological congresses and retired in 1963. During his career he wrote over 300 research papers, which were published in various journals. In addition, he was the author of two books on molluscs (Fischer 1950, 1959).

He received awards for his work from the French Academy of Science (Laureat de l'Academie des Sciences – twice; Commandeur de l'Instruction Publique Palmes Academiques). On top of that, he was awarded the Legion d'Honneur for his services to France (first Chevalier in July1982 and second Officier in October 1998).

Because their children had settled in Australia, Paul and Lynette Fischer retired there in the 1960s. Lynette had been brought up in Sydney from the age of 5 to 17 and Paul knew the molluscan fauna well, as he had made a second trip to Australia at the end of the Second World War.

Paul had always been extremely energetic – almost tireless – and after retirement he worked harder than ever. In 1964 the Great Barrier Reef Committee appointed him as the first Director of the Research Station on Heron Island in Queensland for 1 year. This is now a flourishing establishment run by the University of Queensland.

In 1966 he settled in Mosman on Sydney's North Shore but his travelling did not cease. Between 1966 and 1983 he visited India, Guam, South America, Japan, South Africa, Greece, Portugal, and many other places. When he was in Japan in 1982, he was approached and asked to meet an 'important person'. The meeting had to be incognito and the name of the person was not revealed. It took place on a beach and the person was none other than the Emperor Hirohito, another mollusc enthusiast.

Paul continued the publication of the *Journal de Conchyliologie* until 1979 when it was discontinued. He was made an Honorary Member of the Malacological Society of Australia (as it then was) in 1966. However, he did not restrict himself to writing about molluscs. He also wrote three books representing the reflections of a lifetime upon history, both of his own country and others (Fischer 1980, 1989, 1992). This had always been a subject of absorbing interest to him. The largest of these (Fischer 1989) is a massive book on French history in two volumes, which took 15 years to write.

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BOOK REVIEW

Molecular Systematics and Phylogeography of Mollusks

Edited by Charles Lydeard and David R. Lindberg

Published December 2003, by Smithsonian Institution Press, Washington DC, USA. 328 pages. Hardback. USA$80.00. ISBN: 1–58834–148–8.

This volume makes a contribution to the scientific literature on molluscs that will remain valuable for many years, providing excellent summaries of how studies of DNA sequence variation have informed understanding of the evolutionary relationships and biogeography of molluscs. Nearly all chapters can be considered as the most comprehensive and up-to-date treatments of their respective fields, especially as many include substantial amounts of new data. The editors are to be particularly congratulated on two aspects of the excellent work they have done in the compilation of the volume. These are the choice of contributors and the integration of the book's individual chapters. All of the contributors would be included in any consideration of the most active and insightful researchers in their respective fields.

With regard to the second aspect, much thought was clearly given to the delineation of subject areas, so that overlap between chapters is minimised and most of the subjects suggested by the title are actually covered in the book's pages. Additionally, the effort to format individual contributions consistently has been well rewarded. The presentation of tables in a standardised manner and the equal weight to branches in phylogenetic trees in the several chapters greatly assist legibility. The figures generally are very pleasing – the diagram of mitochondrial gene order (fig. 2.2) makes the complex evolutionary rearrangements of these sequences much easier to understand and the maps of species' distribution and bioclimatic modelling in the chapter by Hugall *et al.* on *Sphaerospira* are striking indeed.

Building on a general introduction on molluscan molecular investigations, the second chapter deals with the implications of such studies for the relationships of the phylum to other multi-celled animals, the inter-relationships of molluscan classes and, since there is a concentration on DNA sequence *per se* in much of the book, on other ways in which molecular information such as gene order or patterns of expression may be informative. The following chapters dealing with the phylogeny of individual groups comprise the bulk of the book. These consider bivalves in general, freshwater mussels, scaphopods, gastropods in general, Euthyneura and opisthobranchs. The book concludes with two chapters on biogeography; one a broad treatment of the topic with respect to aquatic Mollusca and the second a generic-level investigation of the evolution of the terrestrial pulmonate *Sphaerospira*.

Diverse analytical approaches are reflected in the book. In their major investigation of bivalve evolution, Giribet and Distel employ a cladistic approach, using the programme POY, that both aligns the DNA sequences and searches for optimal phylogenetic relationships. McArthur and Harasewych employ maximum likelihood, Bayesian, and supertree techniques in their similarly important study of gastropods. It is not the book's ambit to canvas the merits of the various analyses but the brief introductions to the

techniques offer a valuable recognition of the ongoing developments available to modern systematists.

As a practitioner in molecular systematics, I have encountered many odd ways in which DNA data can be contaminated by sequences of similar genes from other individuals or species. Few are as unusual as the example offered by Steiner and Reynolds in their chapter on Scaphopoda. Although published as a scaphopod sequence, subsequent investigation showed that it actually derived from a sipunculan inhabiting a scaphopod shell. The authors are to be congratulated for both establishing the source of this contamination and making its existence known.

Euthyneuran phylogeny is treated in two chapters. The earlier, by Dayrat and Tillier, concentrates on the implications of molecularly generated phylogenies for the evolution of morphological characters, such as the presence of an operculum, and for general questions, such as the invasion of freshwaters or land. I particular liked the counsel in the introductory paragraph of this chapter that obtaining phylogenetic trees is a preliminary step rather than a goal in the understanding of evolutionary patterns. In this context, attempts to remove the lack of resolution in a tree can be seriously misleading about character evolution. Why this is so critical to Euthyneura is demonstrated in the second chapter on their phylogenetics.

Wägele *et al.* investigate the Opisthobranchia adding substantial amounts of new data to the compilation of DNA sequences available. The basal evolutionary relationships of the group are not clarified robustly by a dataset that must be regarded as impressive, even if only 27 of 178 studied species are represented by all three genes used in the investigation. For instance, the very interesting question of the relationship of opisthobranchs and pulmonates is not resolved. The data includes sequences from more than twenty pulmonates. In the 18S rDNA analysis, the studied pulmonates (Lymnaeidae and Planorbidae) are shown as the sister group (with high probability) to a group of Sacoglossa, Anaspidea, and Cephalispidea. In 16S rDNA analyses, however, the pulmonate representatives are the monophyletic sister group to all of the Opisthobranchia, except Actaeonidae. The data are more informative at slightly lower phylogenetic levels, with consistently high support for several taxa such as Doridoidea and Cladobranchia.

Biogeography is addressed less comprehensively than phylogenetics, with only two chapters and some discussion about the family level in the Roe and Hoeh chapter on freshwater mussels devoted specifically to the subject. Many future investigations will apply DNA sequences to molluscan phylogenetics, so the topic will likely be given additional coverage in any subsequent edition. As the state of knowledge now stands, however, biogeography is a subject where the decision (whether by the editors or individual contributors) to exclude allozyme electrophoretic studies significantly underplays the contribution of genetic studies. The power of combining allozymes with DNA sequence data is shown in the summary by Wares and Turner of the fascinating situation in the *Mytilus edilus* species complex in the North Atlantic. Molecular studies have shown that all the species identified originally by allozyme electrophoresis derive from the Pacific mussel *M. trossulus* following a migration through the Arctic Ocean between three and four million years ago.

The general subjects of Wares and Turner's chapter are the consequences for biogeography and evolutionary diversification of differences between intrinsic and extrinsic factors operating in marine and freshwater habitats. They cite numerous relevant examples – the intriguing case of *Biomphalaria* amongst them.

Hugall *et al.* concentrate on the use of mitochondrial DNA and bioclimatic modelling to investigate the biogeography of a single genus of camaenids in rainforests along the eastern

seaboard of Queensland. The diversity of the group is high, with 24 lineages separated clearly in geography and DNA sequence. The particular details of this investigation are related to several general questions. Amongst these is the relation of the distribution of phylogenetic diversity to biogeographic gaps. This is a methodological advance in conservation biology and a worthy conclusion to the volume.

The collection of DNA sequence data will continue to grow in importance in molluscan studies, as it will in other areas of zoology. Future studies will generally refer to works in this volume: it will continue to be an excellent entree to contemporary molluscan research.

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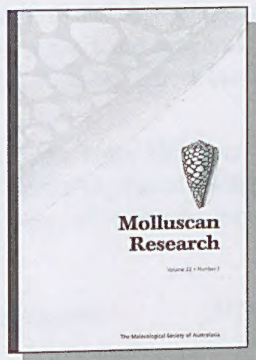
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